Charles University in Prague

Faculty of Mathematics and Physics

BACHELOR THESIS

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Simulace agregačního chování
Simulation of aggregation behavior

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Study programme:	Computer Science
Specialization:	General Computer Science

Prague 2011

In this place, I would like to thank to my supervisor, Mgr. Cyril Brom, Ph.D. for the great effort which he has put forth into supervising of this thesis. Also, I would like to thank to Doc. RNDr. Daniel Frynta, Ph.D. and Mgr. Zuzana Varadínová from Faculty of Science, Charles University in Prague who have helped us with this thesis from the point of view of natural sciences. Last, but not least, I thank to Bc. Edita Dufková and Markéta Popelová for their meticulous proofreading of this text.

I declare that I carried out this bachelor thesis independently, and only with the cited sources, literature and other professional sources.

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In .... date .... Jakub Tomek

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Abstrakt: Mnoho druhů švábů ve volné přírodě tvoří agregace. Tématem této práce je hledání evolučních výhod, které agregační chování švábům poskytuje. Kvůli problémům spojeným s testováním evolučních hypotéz na živých švábech jsme se rozhodli jako prostředek výzkumu použít multiagentní simulaci. Vytvořili jsme několik modelů, které testují určité hypotézy týkající se různých oblastí života švábů. Naše výsledky podporují například hypotézy týkající se ochrany švábů před predátory, či efektivního sdílení potravy z mrtvých švábů. Také nabízíme vysvětlení kanibalismu švábů. Některé hypotézy naopak podpořeny nebyly, např. hypotéza týkající se efektivního využití výkalů jako zdroje jídla. Naše výsledky je možno využít v dalším výzkumu chování švábů. Jelikož je agregace poměrně obecným mechanismem, který se vyskytuje ve více přírodních vědách, naše výsledky lze aplikovat i v nich.

Klíčová slova: švábi, agregace, evoluce

Title: Simulation of aggregation behavior

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Abstract: Many breeds of cockroaches living in nature form aggregations. In this thesis, we are looking for evolutionary advantages provided by the aggregation behavior. Because of the difficulty of testing evolutionary hypotheses on real cockroaches, we decided to use a multi-agent simulation instead. We present several models which test certain hypotheses coming from various areas of cockroach life. Hypotheses on protection against predators, effective use of food from corpses of other cockroaches have been confirmed. Also, we provide an explanation of cannibalism among cockroaches. On the other hand, certain hypotheses were rejected, for example, the hypothesis concerning effective use of feces of other cockroaches. Our results may be used in further research on cockroach behavior. Furthermore, since aggregation as a general process appears in other areas of natural sciences, it is possible to use our results in them as well.

Keywords: cockroaches, aggregation, evolution

Obsah

1. Introduction

An *aggregation* may be defined as any assemblage of individuals that results in a higher density of individuals than in the surrounding area [1, p. 121]. Many animals aggregate, for example ants (army ants in armies, ordinary ants in anthills), termites (in termite mounds), bees (in hives or in swarms), or even people (in houses or in cities).

There are several criteria for classification of aggregations – one of them being the relationship of the aggregated entities [8]. For example, people aggregating (living together) in houses in the countryside tend to be from one family. On the other hand, in larger aggregations (cities), people mostly do not come from one family. The motivation for such an aggregation is different from the motivation for the family aggregation. In this thesis, we are interested mostly in the aggregation of conspecifics, not necessarily of kindred.

In our research, we will study the aggregation behavior of cockroaches. The order of cockroaches inhabits many habitats and shows many behavioral patterns. For example, even though we will study the aggregation of cockroaches, not all cockroaches do aggregate. Members of *thanatophyllum akinetum* avoid other conspecifics. This behavior has been observed in nature [2] and replicated in a laboratory [3]. Most cockroaches do aggregate though and we will study these "social" cockroaches.

How are cockroaches, dispersed in the natural environment, able to form an aggregation? There are two main theories:

The first theory states that when two cockroaches meet, there is a probability they will both stop. After a while, any of them can leave (again, with a given probability). If a cockroach comes to a larger group, the probability of him leaving the group early is smaller [4]. According to this theory, cockroaches are aware of one another via tactile detectors: their antennae. Therefore, an aggregation is a result of many cockroaches being at one place, each of them having a small probability of leaving.

The second theory is based on the presumption of existence of an aggregation pheromone left behind by cockroaches. The cockroaches follow a pheromone trail and such behavior leads to aggregation formation [5]. Aggregations emit more powerful pheromone signal than single cockroaches and therefore it is simpler for other cockroaches to find an aggregation and join it. This theory of the chemical pheromone has been supported by the successful experiment described in [6]. There, small robots marked with a chemical, thought to be the aggregation pheromone, were able to confuse a population of real cockroaches and to alter the behavior of the group. More importantly, without the presence of the pheromone, the robots were not nearly as successful. Therefore, it would seem that the tactile information is not powerful enough to make cockroaches aggregate and the chemical pheromone is necessary indeed.

As we can see, there is a lot of research on the principles of formation of cockroach aggregations. But the question we ask ourselves is not how they aggregate, but why they aggregate instead. Why is it evolutionarily advantageous to aggregate? Or not to aggregate? That is the question. Let's recall the solitary cockroaches of *thanatophyllum akinetum*: Grandcolas [7] has proposed that by dispersing in the environment they protect themselves against raids of army ants. Nevertheless, cockroaches living in human living quarters (e.g., *blatella germanica*) are mostly aggregative.

There are two widely accepted theories on cockroach aggregation. The first is related to the cockroach sexuality. It states that cockroaches aggregate because they can find more suitable sexual partners in this way. We will not work with this theory in this thesis. The second theory is related to protection against predators. There are several reasons how could an aggregation benefit cockroaches in their defense against predators. For example, when cockroach form an aggregation, the odor they create together could be so powerful that it would drive predators away. Or, a single aggregation could be more difficult to find for predators than if they could hunt single cockroaches densely dispersed in the habitat. We will test a hypothesis related to aggregation serving as a protection against predators. However, we try to find other, new reasons for cockroach aggregation formation too; we could say it is the main goal of this thesis.

We are going to formulate several hypotheses on reasons of cockroach aggregation. As we are researching the evolution of aggregation behavior, it is not possible to run the necessary experiments with living cockroaches. To test the formulated hypotheses, we are going to use computational agent-based models. The use of computational models allows us to simulate long era (many generations) of cockroach evolution in a rather short time, no method using real cockroaches is able to do so too[1]. We have decided to use the NetLogo tool [9] for creation of these models, see Figure 1.1. These models have been created in cooperation with Doc. RNDr. Daniel Frynta Ph.D. and Mgr. Zuzana Varadínová from Faculty of Natural Sciences, Charles University in Prague, who have kindly helped us with conversion of reality to agent-based models.

Our hypotheses are divided into several "families". Therefore, there are also several families of models (named *model lines*) created to test these hypotheses. After the preliminary notes on matters common to all the models, every family of hypotheses will be analyzed in a separate chapter. The structure of each chapter is: the hypotheses formulation; the description of models testing these hypotheses[2]; the description of the experiments done with these models; the descriptions of results of these experiments; the discussion of the results.

1.1 Hypotheses overview

In Chapter 3, we will have a look at cockroaches using aggregation as a mean of protection against predation. Chapter 4 consists of research of cockroach food searching strategy (Do aggregated cockroaches search for food more efficiently than cockroaches dispersed in a habitat?), necrocannibalism (Could cockroaches aggregate to get to food from dead bodies of other cockroaches easily?) and

[1] There is a frequent objection against the use of computational models (as opposed to laboratory experiments): Since they are a simplification of real world, their results may be completely different from the reality in nature; only laboratory experiments are reliable. However, experiments done in a laboratory may yield deceitful results too, as in the case of *schultesia lampyridiformis*, when its behavior in a laboratory was different from its behavior observed in nature[8, p. 132].

[2] See Appendix A, for an overview of inputs and outputs of all the models.

coprophagy (Is higher concentration of food from cockroach feces a reason to aggregate?). Chapter 5 consists of research of the phenomenon of cockroach aggressivity (i.e., cockroaches killing and eating one another), we try to explain why a cockroach population does not extinguish itself by killing its members and partly why aggressivity did evolve in cockroaches.

The main goal of this thesis is to test these hypotheses.

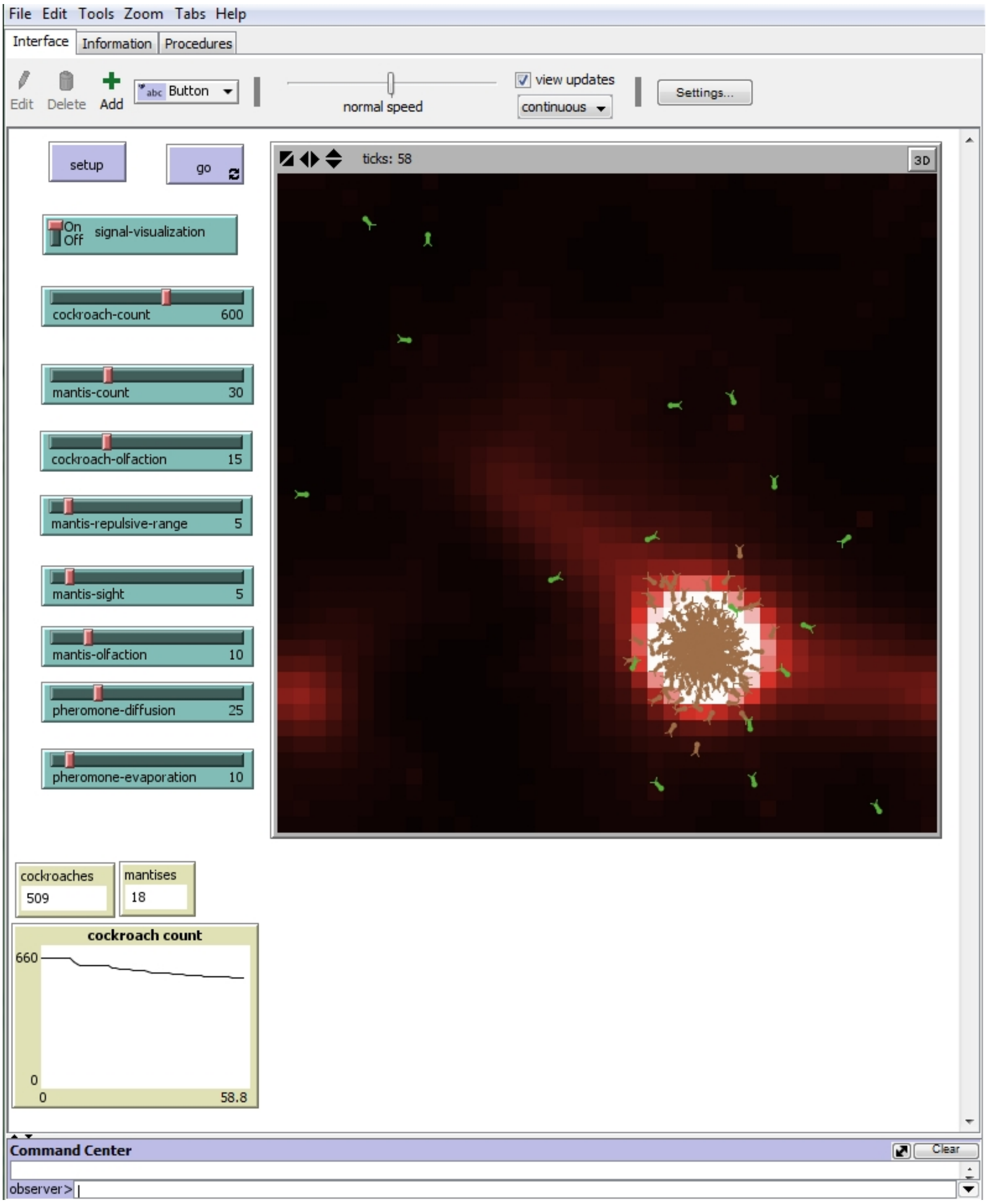

Figure 1.1: An example of a model in NetLogo: Model 1 from Chapter 3, where brown bugs represent cockroaches, green bugs represent mantises. The concentration of chemical pheromone on different patches is visualized by red color (lighter color means higher concentration). NetLogo has its own proprietary programming language (based on Java) which we have used to create our models.

2. Preliminary notes

In this section, several facts common to all of our models are explained.

2.1 Basic terminology

We will do certain experiments with our models. To prevent misunderstanding in what we actually do, let us explain several terms here first. We will demonstrate these on a made-up example of modelling the AIDS spreading throughout the world in 2000–2011:

- a run: A single computation of a model: Simulating era of 2000–2011 in a single observed place (e.g., Prague) once.
- an experiment: A batch of runs which is analyzed together: Simulating era of 2000–2011 in all observed places (cities, villages, etc.).
- a subexperiment: Sometimes, an experiment may be logically subdivided into several smaller sets of runs and these are called “subexperiments”: We could be interested only in spreading of AIDS in Africa, for example. Then the subexperiment would be the simulation of 2000–2011 in all observed places from Africa only. Another subexperiment would be if we were to observe the AIDS spreading among the top 5% wealthiest people in the world.

2.2 The space and time representation

As we have decided to use the NetLogo tool for creating simulations, we use the standard NetLogo representation of the environment. The simulation environment is a rectangle composed of little squares – *patches*. All patches have integer coordinates. Agents inhabiting the environment have real[1] coordinates, i.e., more agents can be on a single patch while having slightly different coordinates. Let us note here, that our modelled agents make steps of integer length, but as they may turn around freely, real coordinates are necessary.

Time in all our models is discrete. A single unit of time is called a *tick*.

2.3 Model description

When creating an agent-based model, it is necessary to describe it appropriately. When described well, a model can be understood, reimplemented and even criticized effectively and correctly. As the technique of agent-based modelling grows in popularity, many new models are created. Without a certain degree of standardization, it may be very difficult to compare them and evaluate which are useful and which are not. For these reasons, we have decided to use the revised ODD[2] protocol [10, 11] for the description of our models.

[1] Limited to Java float.

[2] **O**verview, **D**esign, **D**etails

In order to fully understand our description of the models, we recommend to become familiar with the ODD protocol. The structure of the ODD protocol may be briefly described in this way:

- Overview:
  - Model purpose
  - State variables and scales
  - Process overview and scheduling
- Design concepts (emergent behavior, adaptation, interactions between agents, etc.)
- Details
  - Initialization
  - Input
  - Submodels (This does not describe variants of the basic model, instead, it describes the details of processes running in the model.)

Certain mechanisms are unchanged across several of our models. To avoid unnecessary text duplication, we shall reference these parts between chapters.

2.4 Behavior diagrams

The environment is inhabited by agents. These agents are controlled by their action-selection rules. There are two major ways of writing such action-selection rules – a pseudocode, or a diagram. In this thesis, we use diagrams as we feel they are generally easier to understand. We represent agents as finite state machines (FSM). In our diagrams, an agent starts the tick in the "The start of a tick" state and ends in the "The end of a tick" state (or he dies). In the next tick, he will again start in "The start of a tick" state. There are three different elements in our action-selection diagrams:

- Rectangular boxes: These boxes contain an action (e.g., walking, eating, etc.). After an agent has performed all the actions in the box, he decides upon his next action: he follows an edge leading to another state (unless he is in the final state). The decision is determined by the conditions specified on edges leading from a box. If only one edge leads from a box, there is no decision made and this edge is always used.
- Diamond boxes: Sometimes, the action to be performed can not be chosen yet and more decisions need to be made. Such an "intermediate state" is represented by a diamond box.
- Edges: Transitions between states are represented by edges. The condition, upon which an edge is chosen, is written on the edge label.

See Figure 2.1 for a demonstration.

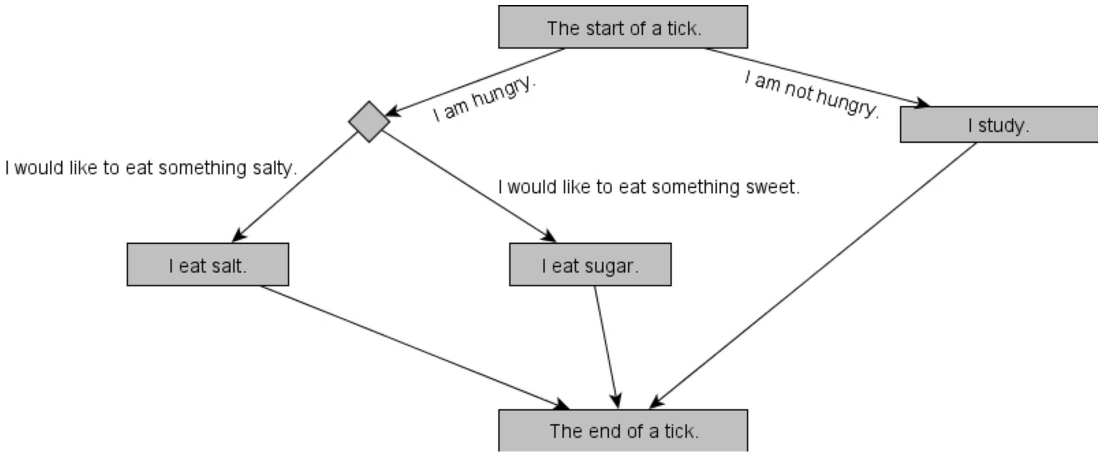

Figure 2.1: This is an example diagram of action-selection rules of a simple student in a single tick. At the beginning of the tick, the student decides whether he is hungry or not. If he is not, he studies (and then finishes the tick). If he is hungry, he further decides whether to eat salty or sweet food, eats it and then finishes the tick too.

2.5 Agent reproduction

Agents reproducing in our models reproduce by binary fission. This is an abstraction of real (sexual) reproduction of modelled agents, which is overly complicated for the sake of our models. Furthermore, the aggregation which we study could be beneficial from sexual reasons (more partners for mating), therefore if the aggregation behavior of agents has emerged, it would be difficult to know whether it was for reasons of our hypotheses, or for sexual reasons.

2.6 A convention for writing state variables

Our models contain many state variables mentioned in this text. To distinguish names of those state variable names from an ordinary text, names of state variables are printed by a `special font`.

2.7 A convention for writing random numbers

In the text and in diagrams, “random x” is sometimes used. Such a syntax means a random element of $[0, x) \cap \mathbb{Z}$. Accordingly, “random float x” means a random element of $[0, x) \cap \mathbb{R}_p$, where $\mathbb{R}_p$ are pseudo-real numbers (limited to the range of Java float).

2.8 About state variables in models

Our models are characterized by certain state variables: values, which change the behavior of the environment or the behavior of agents (e.g., how much food is added to the system in every tick or how much do agents reproduce).

There are three types of "state variables" we use to characterize the experimental environment and entities inhabiting it:

- *constants*: Their value is held fixed throughout the experiment.
- *parameters*: Their value may be set by the experimenter at will, but it does not change on its own. E.g., an experimenter may set the probability of cockroach reproduction, run the experiment and collect its results. Then he may change its value, run the experiment again and see, how differently the model behaves. This is different from constants which are held fixed throughout both of these experiments.
- *variables*: Their value may change when a simulation runs (for example, the number of cockroaches often changes if cockroaches may reproduce or die).

There are two hierarchical levels of variables, the environment (global) variables being the first one. The second level consists of entity variables: patch variables and variables of individuals living in the environment.

2.9 Boxplots

We have used standard boxplots to depict most of our results. The box ranges from 25-percentile to 75-percentile and whiskers range from minimum to maximum of measured values.

3. Model 1: Mantises and cockroaches

In this chapter, we will study impacts of aggregation on the ability of cockroaches to survive in an environment with predators. Let's consider two breeds of agents living in an environment: cockroaches (prey) and mantises (predators). Mantises eat cockroaches. This chapter explores the possibility of an aggregation serving as a mean of prey protection against predation. There are two theories on aggregation mechanism mentioned in the introduction of this thesis: the chemical pheromone theory and the tactile mechanism theory. We will presume the chemical theory is true. Then, cockroaches emit an aggregation pheromone. The benefit for cockroaches is that they can track one another and form aggregations when following the chemical gradient. The problem is that mantises may be able to follow the chemical gradient too. In nature, it has been observed that mantises are *strongly solitary*. This means they avoid other mantises (except when mating) [12, p. 256].

3.1 Hypothesis formulation

We hypothesize that the aggregation may serve as a mean of protection against predation via spatial distribution. Let's consider a hypothetical case, where the universe is divided into 100 mantis territories, each containing one mantis. Mantises are reluctant to go into territories of other mantises due to their solitariness. If there are 100 cockroaches in the universe, each inhabiting one mantis territory, when the mantises get hungry, each of them will have something to eat (even though it may take some time to find the single cockroach in the territory). On the other hand, another extreme is when these 100 cockroaches are aggregated in only one mantis territory. This way, only one mantis can eat a cockroach, as other mantises do not want to go to this mantis' territory. For the "lucky" mantis, it will be simple to find the aggregation (due to a strong chemical signal coming from the aggregation; mantises are able to smell the pheromone) and to kill a cockroach. However, 99 mantises will not eat anything. This is very good for the cockroach population and very bad for the mantis population (mantises would probably start attacking one another trying to get food).

We propose that if mantises are unwilling to approach other mantises, then the aggregation is beneficial to the cockroaches, for more of them will survive in the way described in the paragraph above.

3.2 Model description

3.2.1 The purpose

The purpose of this model is to test the above stated hypothesis, i.e., to confront two influences of cockroach aggregation on their ability to survive. The first influence is negative (for cockroaches): when they form an aggregation, it is easier for a mantis to find the aggregation and kill a cockroach. The second influence is positive: since mantises are strongly solitary, fewer mantises will be able to get to the aggregation.

3.2.2 Entities, state variables and scales

There are two breeds of agents inhabiting the environment: mantises and cockroaches.

All state variables and their initial values are written in Table 3.1.

3.2.3 Process overview and scheduling

Within every tick, several phases are processed in the following (given) order:

1. Agents (mantises and cockroaches) add a certain amount of the pheromone to the environment.
2. The chemical pheromone disperses in the environment.
3. Cockroaches move.
4. Mantises move
5. A part of the chemical pheromone evaporates.

The order of cockroaches and mantises in which they act in every tick is random. However, it is given, that cockroaches act before mantises.

3.2.4 Design concepts

Emergence

We expect cockroaches to form aggregations — the number and the size of these aggregations being dependent on the range of cockroach smell. If the aggregation behavior emerges, it may be used to measure the effect of the aggregation on the protection against predation.

Adaptation

Agents are not adaptive. Instead, we set different values of environment parameters and measure the resulting state of the environment.

Objectives

The objectives of cockroaches is to follow the chemical gradient, thus forming aggregations. The objectives of mantises is to be not hungry. There are no individual fitness values for our agents. Instead, we consider global fitness of the cockroach population (the number of cockroaches surviving the experiment) and global fitness of the mantis population (the number of mantises surviving the experiment).

Name	Type	Description	IV
`width of the universe`	e. c.	How wide (in patches) is the environment.	40
`height of the universe`	e. c.	How high (in patches) is the environment.	40
`pheromone dispersion rate`	e. c.	Determines how much pheromone disperses every tick.	25
`pheromone evaporation rate`	e. c.	Determines how much pheromone evaporates every tick.	10
`mantis sight`	e. c.	The range of mantis sight	5
`mantis olfaction`	e. c.	The range of mantis olfaction.	10
`pheromone added`	e. c.	How much pheromone does a single agent add to the environment in a single tick.	10
`maximum food of mantises`	e. c.	The maximum amount of food a mantis may contain. This value is reached when she eats something.	10
`mantis step length`	e. c.	How far does a mantis walk in a single move.	2
`cockroach step length`	e. c.	How far does a cockroach walk in a single move.	1
`counter maximum`	e. c.	The maximum value of mantis state counters (hunger/walking).	5
`repulsive range`	e. p.	The size of a mantis territory.	-
`cockroach olfaction`	e. p.	The range in which are cockroaches able to detect the concentration of the pheromone).	-
`number of cockroaches`	e. v.	How many cockroaches are in the environment.	600
`number of mantises`	e. v.	How many mantises are in the environment.	30
`amount of pheromone`	p. v.	How much pheromone is on a patch.	0
`mantis state`	m. v.	Whether a given mantis is currently walking or waiting.	waiting
`hunger counter`	m. v.	How hungry a mantis is	10
`walking counter`	m. v.	How many next ticks will a mantis walk.	0
`waiting counter`	m. v.	How many next ticks will a mantis wait.	5

Table 3.1: Initial values (IVs) of constants and variables are written in this table. The first letter of Type determines whether the state variable belongs to the environment (e.), patches (p.), cockroaches (c.) or mantises. The second letter of Type determines whether it is a constant (c.), a parameter (p.) or a variable (v.). Parameter values must be specified by the experimenter, they have no given initial value.

Sensing

Cockroaches can only smell the chemical pheromone. Mantises can smell it too, furthermore, they are able to see cockroaches in a given range. Mantises know when they are too close to another mantis.

Interaction

When hungry, mantises prefer to eat cockroaches, when no cockroaches are around, they try to eat other mantises. Note that in this model, these interactions (mantises killing cockroaches or other mantises) are the only ways any agents may die. Aging or starving to death are not included in this model.

Stochasticity

The stochasticity is a part of the model. Cockroaches sometimes tend to aggregate with other cockroaches, sometimes they wander randomly. We chose to model certain „decisions“ of agents probabilistically as we cannot yet understand the precise mechanisms ruling such decisions. Because it is currently impossible to know exactly how a cockroach brain works, we have tried to make the cockroach behavior look plausible, even though precise mechanisms of their behavior in nature may be different.

Collectives

Cockroaches form aggregations. This group formation is spontaneous though (i.e., the aggregations are the result of individual behavioral rules, there is no „higher force“ ruling them to aggregate).

Observation

We observe three variables: The number of cockroaches, mantises and non-hungry mantises surviving the experiment (200 ticks).

3.2.5 Initialization

State variables have deterministic initial values (written in Table 3.1). These values have been chosen arbitrarily. In the case of state variables representing the state of real nature (e.g., how much energy do cockroaches burn by sitting per unit time), empirical values are unknown to our knowledge. We have aimed for such values, which lead to reasonably plausibly looking behavior.

3.2.6 Input data

The model does not use input data to represent time-varying processes[1].

[1] This sentence has been recommended by the authors of revised ODD protocol to be used in a situation, when no external data are used to represent changes in processes over time [11].

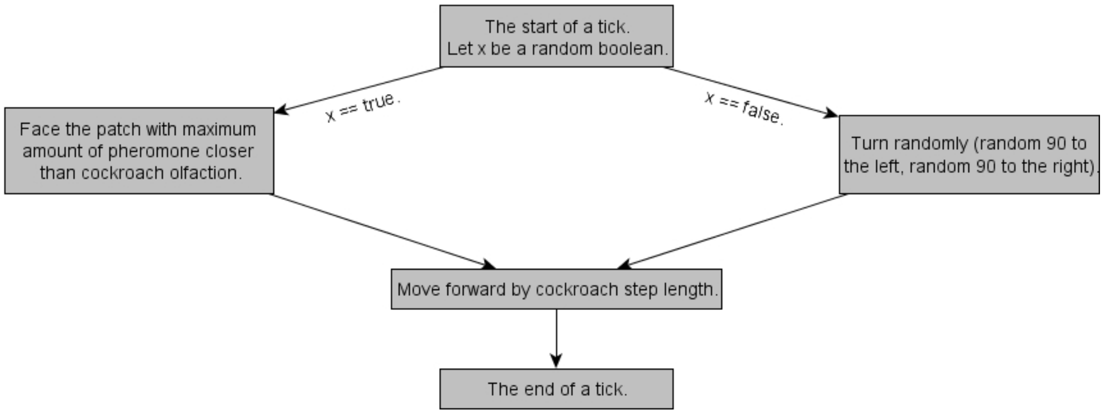

Figure 3.1: The diagram describing cockroach action-selection rules.

3.2.7 Submodels

At the beginning of this section, let's note we did not aim for perfectly plausible model of the cockroach aggregation. The aim of this model is not to determine how cockroaches aggregate. We concentrate on this: when they aggregate, does it give them an advantage? In other words, we are interested in impacts of the aggregation, not so much in the principle underlying it.

Pheromone dispersion

In this phase, representing the phase 1 of 3.2.3, all patches add certain amount of their chemical to their neighbours (in 4-neighbourhood). The amount is described in this way:

$$amount = \frac{pheromone \cdot dispersion}{1000}$$

where *pheromone* is the value of the patch variable `amount of pheromone` of the dispersing patch. *Dispersion* is the environment constant `pheromone dispersion rate`.

Pheromone addition

In this phase, representing the phase 2 of 3.2.3, all agents (cockroaches and mantises) add `pheromone added` units of pheromone to the patch they are standing on. This way, together with the Pheromone dispersion phase, aggregations tend to generate strong chemical gradient, as opposed to cockroach solitaires.

Cockroach movement

This phase represents phase 3 of 3.2.3. Action-selection rules of cockroaches (for one tick) are described in Figure 3.1.

Cockroaches in this model are very simple: half of the time they walk randomly, half of the time they aggregate. The probabilities of walking randomly or towards an aggregation, were chosen arbitrarily. We aimed for plausibly looking aggregation. If cockroaches have aggregated all the time, they would form tiny aggregations at the beginning of the experiment and would not move since.

Mantis movement

This phase represents phase 4 of 3.2.3. Action-selection rules of mantises (for one tick) are described in Figure 3.2. Although the behavior could seem overly complicated, it is actually rather simple. The general idea is: A mantis sometimes sits, sometimes walks. She rotates only when she starts walking. I.e., after she starts walking, she walks in a straight line until she stops again. Then, she waits a while, rotates and walks again.[2]. Some time after a mantis has eaten something, she will become hungry. In our model, mantises cannot die of hunger, i.e., they can be hungry for infinitely long time. How mantises react to hunger depends on whether they are currently sitting or waiting.

When sitting, a mantis is resting, when hungry, she eats something only when it comes near the mantis (cockroaches are preferred over mantises). The distance in which a mantis attacks is equal to `mantis step length`.

When a mantis is in walking state and becomes hungry, she starts looking for food. Mantises prefer to eat cockroaches they can see. If they can not see any, they eat mantises they can see. If they can not see any such mantises, they follow the chemical pheromone gradient.

This described behavior is used when mantis is not too close to another mantis (i.e., when the nearest mantis is further than `repulsive range`. When another mantis is too close, our mantis tries to go away from her. To prevent confusion, we would like to emphasize that `repulsive range` is used only in this place, it is not related to `mantis sight` and `mantis olfaction` which are used when a mantis tries to find food.

This description was only a short overview, to make reimplementation possible, we decided to include full action-selection rules of mantises in the Figure 3.2.

It could be argued why the attack of mantises is ranged (with range `mantis step length`). The issue is with mantises being unable to attack their prey otherwise. For example, let us consider a scenario with a hungry mantis and a cockroach on an adjacent patch and. The mantis wants to attack the cockroach. With too small range of her attack, she would have to move near the cockroach and with her rather long step, would leap over the cockroach and she would be too far away from him again. The range we have used prevents this problem and also represents the fact that mantises may move when attacking. I.e., when a mantis attacks on range 1.9, she is not considered attacking at such a range, instead, she is considered to move a bit, kill the prey in close combat and then return back to the place where the mantis was previously.

Pheromone evaporation

In this phase, representing the phase 5 of 3.2.3, all patches subtract certain amount of the chemical pheromone present on them (this simulates the evaporation of the pheromone). The amount of pheromone which evaporates is measured in percents and is given by the environment constant `pheromone evaporation rate` (i.e., with the currently used value, 10% of the pheromone on all patches disappears).

[2]This behavior of walking in a line, waiting, turning and walking in a line again has been observed in nature (Daniel Frynta, personal communication, 18.5.2011).

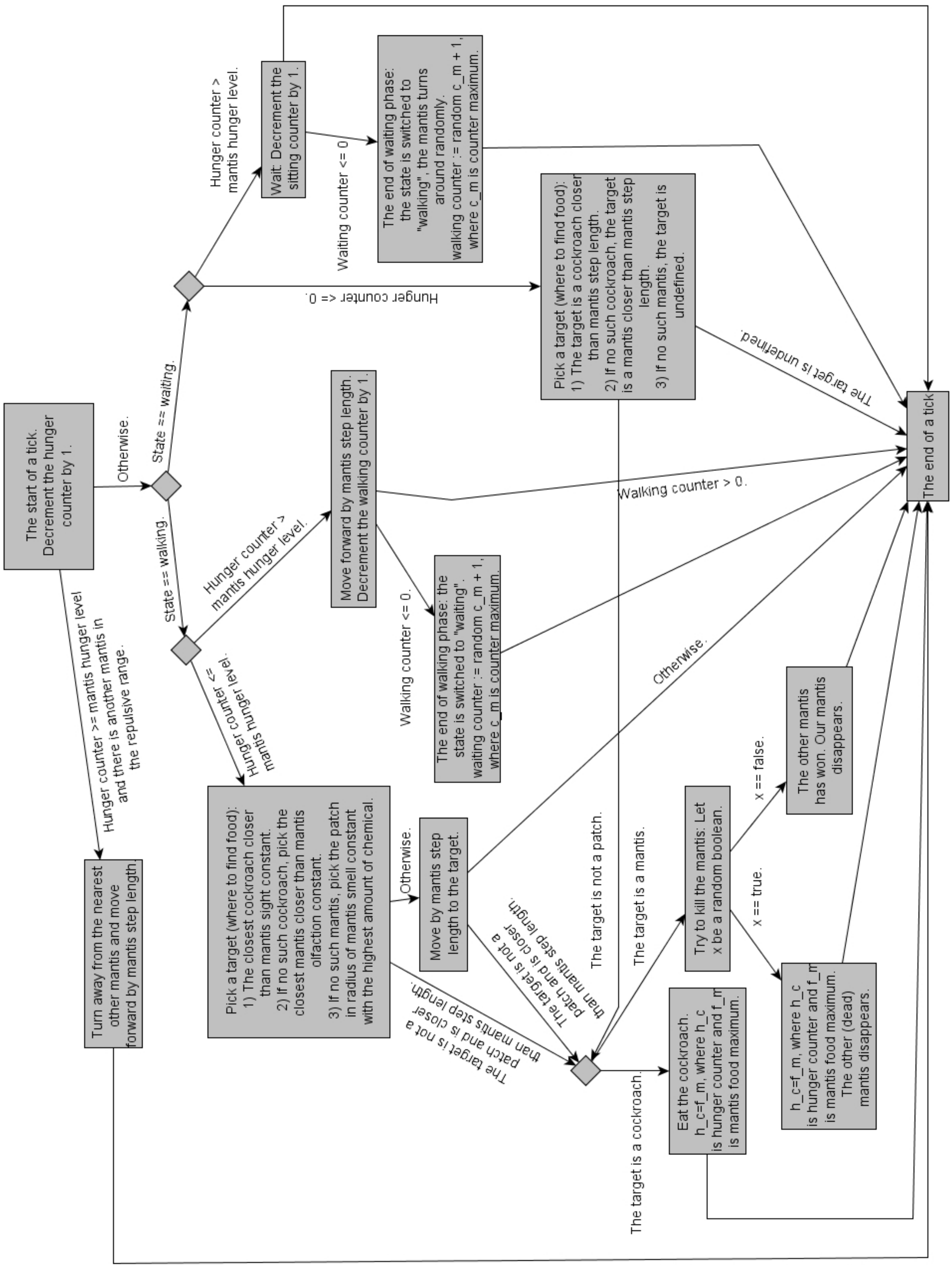

Figure 3.2: The diagram describing mantis action-selection rules.

3.3 Experiment description

The experiment consists of the initialization and the run of 200 ticks. We examine the number of cockroaches and mantises at the end of the experiment. Another thing measured is the number of non-hungry mantises at the end of the experiment. Since we have neglected death of hunger, we should measure it too. It is very different if 30 mantises survive and they are all full of food, or when 30 mantises survive and they are all very hungry.

There are two parameters are changing the behavior of the model (`cockroach olfaction` and `repulsive range`). To understand the behavior of the model under various circumstances, we have ran it with several different values of parameters, see Table 3.2. This way, we were able to see impacts of parameter combinations on the number of surviving cockroaches and mantises.

We have made an observation that the higher the `cockroach olfaction` is, the less aggregations are formed[3] (i.e., `cockroach olfaction` = 1 means that very many small aggregations will be formed, `cockroach olfaction` = 20 means that only one large aggregation will be formed). This way, we are able to control the number of aggregations formed, while they are still formed by individual decision rules.

For better statistical credibility, all subexperiments have been repeated 100 times.

Parameter name	Values
`cockroach olfaction`	0; 2; 4; 6; 8; 10; 12; 14; 16; 18; 20
`repulsive range`	0; 2; 4; 6; 8; 10; 12; 14; 16; 18; 20

Table 3.2: Various values of parameters. Each value of `cockroach olfaction` is paired with each value of `repulsive range`, so there are 121 different combinations.

3.4 Results

As we have two parameters affecting the number of surviving mantises and cockroaches, we decided to depict the results using 3D plot. The number of surviving cockroaches, surviving mantises and surviving non-hungry mantises is shown in Figure 3.3[4].

Let us recollect that high values of `cockroach olfaction` lead to several large aggregation being formed, while small values lead to the formation of many small ones.

An important result is, that growing `cockroach olfaction` leads to a higher number of surviving cockroaches. The importance of `repulsive range` is surprisingly low for cockroaches (we try to explain this phenomenon in Discussion of this chapter).

[3]See appendix B, section .4 for an overview of dependence of the number of aggregations formed on `cockroach olfaction`

[4]As we could not depict variations of measured variables in the 3D plot, we have included a table of them in Appendix B, section .5

On the other hand, the importance of `repulsive range` is rather high for mantises. When mantises are territorial, i.e., `repulsive range` is larger than 0, much more of them survive and, which is very important, much more of them survive non-hungry. To a certain extent, the larger the territory, the better for them. There is a boundary of `repulsive range`, being something around 8. Above this level, the territoriality does not get any more advantageous The reason is, that mantis territories are so large that mantises are protected from one another well enough. Further explanation could be that the space in the environment is limited. If `repulsive range` has been 100 with width and height of the environment as it is now (40x40), the behavior of mantises would be the same as if it has been 80 - all mantises would repulse one another in both cases.

Let us note that our results do not depend too heavily on values of `mantis sight` and `mantis olfaction`. Unless they are very small (0 or 1), the difference in results is little.

3.5 Discussion

The hypothesis that the aggregation serves as a protection against strongly solitary predators has been supported by our data. The aggregation is heavily advantageous to cockroaches almost independently on the predator solitariness (i.e., the presumption of solitariness was not necessary).

It seems there are two influences of mantis territoriality on cockroaches which have canceled each other: The first influence is that when mantises are not territorial, more of them may attack an aggregation as they don't repulse one another so much(which is bad for the aggregation). The second influence is, that when mantises are not territorial, they kill one another much more (especially when they are all near a single aggregation), therefore there are less mantises in the environment in total.

For mantises, it is better to be territorial as more of them survive. Furthermore, if cockroaches are not highly aggregative, mantises will generally have more food as each mantis will have cockroaches around to eat. When we designed this model, we concentrated on cockroaches. However, we think that this "emergent observation" of mantises is interesting too. It could explain why many predators form territories: it is simply too disadvantageous to kill one another and territory formation prevents that. A generalization may be made here: we don't have to consider single agents only. A herd of animals is, from a certain point of view, one entity. A zeal of zebras may be represented by our "cockroach" and a pride of lions may be represented by our "mantis". At a certain level of abstraction, the behavior of our model is plausible – in nature, lions' prides are solitary (however, zeals of zebras do not aggregate).

Further work could examine the influence of cockroach aggregation as a mean of protection against predators who can not smell the cockroach aggregation (we expect that the aggregation would prove even more advantageous). Another experiment could be done with predators behaving like army ants. It would be interesting to see if behavior similar to the behavior of *thanatophyllum akinetum* would be the most advantageous to our virtual cockroaches.

Another thing which could be done differently, would be the measurement of the number of non-hungry mantises in the experiment. We have measured this number at the end of 200th tick. Therefore, it could have happened (it is very unlikely though) that all mantises were hungry until tick 199, in which they all ate and therefore all mantises were non-hungry at the end of the experiment when we measured it. We tried to prevent this phenomenon from confusing our data by repeating the experiment 100 times, which, we believe, should be enough. However, instead of measuring the number of non-hungry mantises at the end of tick 200, a "discrete integral" over all 200 ticks of the experiment could be counted and evaluate instead of the state at the end of the experimental run.

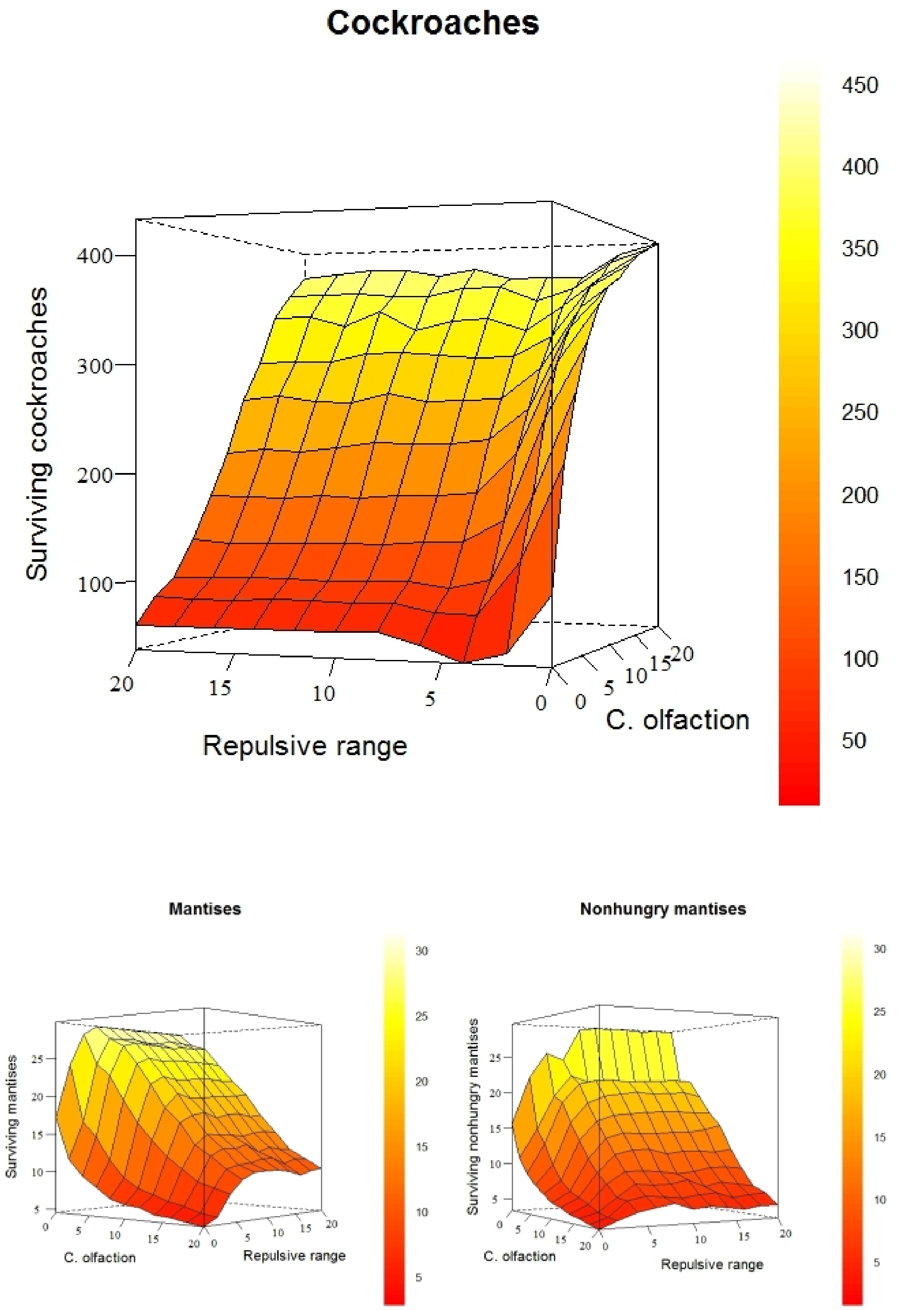

Figure 3.3: The wireframe showing the average number of cockroaches surviving the experiment(top); mantises surviving the experiment (bottom left); nonhungry mantises surviving the experiment (bottom right). These values are dependent on `cockroach olfaction` and `repulsive range`. We work with a mean of 100 repeated runs. Note that labeling of axes is different for cockroaches and for mantises.

4. Model line 2: Food searching, necrocannibalism and coprophagy

In this chapter, we will study eating habits of cockroaches, namely how they search for food and how important is necrocannibalism and coprophagy to an aggregation[1].

4.1 Hypotheses formulation

4.1.1 An improvement of food searching strategy

The first hypothesis relates to the food searching strategy of cockroaches. The work of Durier and Rivault [14] suggests that cockroaches are not capable of smelling distant food. If a cockroach does not consider other cockroaches in his decisions, he has to search for food randomly. However, if a cockroach does consider other cockroaches when deciding, could not he use the information about their positions? According to our first hypothesis, he could.

We propose that a hungry cockroach could go further from places with high concentration of pheromone (because that is how we think he knows about large number of cockroaches). The cockroach could expect that where other cockroaches are, there is no food, as they have already eaten it.

It could seem, this is an anti-aggregative behavior. However, the key action of cockroaches is, that when not hungry, they try to aggregate (they go to the place with the highest pheromone concentration they can find). The purpose for such behavior is, that the aggregation creates a strong chemical gradient. Using the gradient, cockroaches going out of the aggregation are able to leave the aggregation space (where there is no food) effectively and to find food quickly (and then return quickly).

Hypothesis summary: We propose that the style of behavior “hungry means out, full means in” is more effective than random search for food without aggregation.

4.1.2 An effective use of corpses

The second hypothesis relates to the distribution of dead cockroaches in the environment. It has been observed that many cockroaches are necrocannibals, i.e., they eat dead conspecifics to keep the necessary amount of proteins in their body[8, p. 71-73]. This behavior is mostly present in habitats with low amount of proteins in food (note that this may be said about human cannibalism). Sometimes, cockroaches even attack other cockroaches to kill them and eat them. We study such aggressive behavior in Chapter 5.

The second hypothesis states that in places with very high concentration of cockroaches will be high concentration of dead cockroaches too. High concentration of dead bodies means a lot of food, which is energetically valuable and easily

[1] Certain parts of this chapter have been covered in [13]. This text is revised and more in-depth however.

found. This leads to lesser amount of energy spent on finding the food outside the aggregation.

Hypothesis summary: We propose that if cockroaches are necrocannibals, it is more effective to be social as social cockroaches will often find food from dead conspecifics in an aggregation. Because social cockroaches are concentrated in aggregations, we expect a higher concentration of dead cockroaches in aggregations too.

4.1.3 An effective use of feces

The third hypothesis relates to the distribution of cockroach feces in the environment. It has been observed that cockroaches (especially nymphs[2]) often feed on feces of adults [8, p. 78]. It is a way of passing proteins to young cockroaches, without them having to leave the aggregation. It has been shown that nymphs fed by feces containing proteins were able to survive longer than nymphs which have not [15].

The hypothesis is similar as the hypothesis 4.1.2: there is much higher concentration of cockroaches in the aggregation than outside it. Therefore there will be higher concentration of easily found food (feces) in the aggregation.

Hypothesis summary: We propose that if cockroaches eat feces of conspecifics, it is more effective to be social as social cockroaches will often find food feces of fellow cockroaches in an aggregation. Because social cockroaches are concentrated in aggregations, we expect a higher concentration of feces in aggregations too.

4.2 Model description

There are three different hypotheses, yet the models used to test them are very similar. For this reason, we will describe only the simplest of the model line 2 (i.e., the model used to test the first hypothesis) in this section. The variations used to test the other two hypotheses are described in the next section. As far as we know, there is no standard way of describing such model variations (although the authors of [11] did consider something like Δ-ODD protocol).

4.2.1 The purpose

The purpose of this model is to test the food-searching strategy of cockroaches described in 4.1.1. It is very important that the model is designed to be easily adjustable to test hypotheses in 4.1.2 and 4.1.3.

4.2.2 Entities, state variables and scales

There is only one breed of agents inhabiting the environment – cockroaches.

All state variables and their initial values are written in Table 4.1. Here, some of them are discussed more in depth:

[2]Nymphs are young cockroaches.

The `energy from food` constant determines how many units of energy does a cockroach get from one unit of food. There obviously could be only food or only energy, but we chose this way for possible future extension of the model. In the extension, there could be different amount energy gained from one unit of generic food from one unit of food from other cockroaches (corpses or feces).

The two food thresholds are a way of getting more plausible behavior. When `energy` of a cockroach gets below `low threshold`, the cockroach becomes hungry. He ceases to be hungry when he finds enough food to make his `energy level` higher than `high threshold`. This behavior results in more plausibly looking behavior than with only one threshold determining whether a cockroach is hungry (below the threshold) or not (above the threshold). With only one threshold, cockroaches oscillate around the single threshold and their behavior does not look very believable as they switch between hungry and non-hungry states too often. Why have we chosen the values of energy thresholds we have? Obviously, `low threshold` has to be high enough so cockroaches have enough time to find food. Furthermore, to prevent the above mentioned oscillation, we set `high threshold` to a rather large value.

The `minimum food threshold` constant determines the minimum amount of food a cockroach finds interesting to eat. Without this parameter, cockroaches behave somewhat suicidally. Since there is a price paid (in energy units) for eating, if a cockroach eats too little food, he pays for it. If he pays like this for a long time, he will die eventually. `Minimum food threshold` assures that a cockroach eats only when it is energetically advantageous to him. The value 0.3 means that a cockroach will eat only if he gains at least 1.5 point of energy (0.3*energy from food), which is almost completely burned by the act of eating. The rest (0.5 points of energy) statistically compensates the fact that cockroaches often have to move to the food, thus burning even more energy. With `minimum food threshold` = 0.3 is net growth of energy in a tick still small, but the cockroach does not lose any energy, which is important.

`Sociality` of cockroaches is the crucial variable in our model. It is evolved (slightly changed between generations) and it determines how "social" a cockroach is. Let's note that the social behavior is not always the same as the aggregative behavior. In our model, sociality means how much does a cockroach consider the signal of other cockroaches in his decisions. To emulate the food-searching behavior described in 4.1.1, when hungry, social cockroaches go from the strongest source of chemical signal he's able to smell, while when not hungry, they go towards it. We expect that it to lead to aggregation formation. The sociality is not binary, instead, it works probabilistically. The scale of the variable is 0-10 (it is integer), where 0 means that the cockroach is always asocial, 10 means that he is always social. When we later mention "social cockroaches", we mean the cockroaches currently behaving socially[3].

When cockroaches are trying to find an aggregation (or they are running away from it), they use `cockroach olfaction`. For technical reasons, we have chosen a value which could be surprisingly high. Without it however, a cockroach is often confused by his own pheromone and behaves strangely. A possible future work could be to change the mechanism of spreading the pheromone so

[3]For example, cockroaches with `sociality` = 10 are always social, with `sociality` = 8, they are social 80% (statistically) of their lives, with `sociality` = 0, they are never social.

the self-confusing behavior would not happen. Nevertheless, since the behavior of cockroaches on macroscopic level looks plausibly, we do not think that the mechanism we currently use would be a large problem.

Name	Type	Description	IV
`universe width`	e. c.	How wide (in patches) is the environment.	40
`universe height`	e. c.	How high (in patches) is the environment.	40
`pheromone dispersion rate`	e. c.	Determines how much pheromone disperses every tick.	25
`pheromone evaporation rate`	e. c.	Determines how much pheromone evaporates every tick.	10
`pheromone added`	e. c.	How much pheromone does a single cockroach add to the environment in a single tick.	10
`cockroach olfaction`	e. c.	The range in which are cockroaches able to detect the concentration of the pheromone	5
`energy from food`	e. c.	How much energy is gained from one unit of food	5
`maximum energy level`	e. c.	The maximum amount of energy a cockroach may have.	100
`low threshold`	e. c.	With `energy` below this threshold, a cockroach becomes hungry.	30
`high threshold`	e. c.	With `energy` below above this threshold, a cockroach becomes not hungry.	70
`cost of sitting`	e. c.	How much energy a cockroach burns when he sits.	0.5
`cost of eating`	e. c.	How much energy a cockroach burns when he eats.	1
`cost of walking`	e. c.	How much energy a cockroach burns when he walks.	2
`minimum food threshold`	e. c.	When the amount of food on a patch is lesser than this, a cockroach won't eat it.	0.3
`maximum age`	e. c.	The age when a cockroach dies of age.	500
`step length`	e. c.	How far does a cockroach walk in a single move.	1
`food growth`	e. p.	The amount of food added to every patch in a tick.	-
`number of cockroaches`	e. v.	How many cockroaches are in the environment.	20
`pheromone amount`	p .v.	How much pheromone is on a patch.	0
`food amount`	p. v.	How much food is on a patch.	1
`sociality`	c. v.	How social a cockroach is.	[4]
`age`	c. v.	How old a cockroach is.	0
`energy`	c. v.	The energy level of a cockroach.	100
`state`	c. v.	The state of a cockroach: hungry(0) or not(1).	1

Table 4.1: Initial values (IVs) of constants and variables are written in this table. The first letter of Type determines whether the state variable belongs to the environment (e.), patches (p.) or cockroaches (c.). The second letter of Type determines whether it is a constant (c.), a parameter (p.) or a variable (v.). Parameter values are set by the user, they have no given initial value.

4.2.3 Process overview and scheduling

Within every tick, several phases are processed in the following (given) order:

1. Food is added to the environment.
2. The chemical pheromone disperses in the environment.
3. Cockroaches add certain amount of the pheromone to the environment.
4. Cockroaches move (and they eat).
5. Cockroaches reproduce.
6. Cockroaches age.
7. A part of the chemical pheromone evaporates.

The order of cockroaches in which they act in every tick is random.

4.2.4 Design concepts

Emergence

We expect that high `sociality` of cockroaches could evolve, leading to aggregation formation. However, it is not certain how many aggregations will emerge and how many cockroaches will aggregate.

Adaptation

Our agents are not adaptive in their life, their `sociality` may change between generations though.

Objectives

The objective of all the cockroaches (social and asocial) is to find food when they are hungry. Social cockroaches have a further objective – to aggregate with other cockroaches when not hungry. When these objectives are fulfilled, a cockroach sits and waits[5].

Sensing

Cockroaches are able to smell the pheromone in a given range. They are also able to detect that the food is on a patch adjacent to the patch they are standing on. Social cockroaches indirectly "know" where food is not via smelling the signal of other cockroaches.

[4] The value is randomized on the scale 0-10.

[5] This means that well-eaten cockroaches do not explore the environment; this presumption does not have to be necessarily true in nature.

Interaction

There is no direct interaction between single cockroaches such as information transfer, attacks etc. Indirect interaction would be sensing the pheromone signal of other cockroaches.

Stochasticity

The stochasticity is a part of the model. The decision whether a cockroaches behaves socially or asocially is probabilistic. Also, the reproduction of cockroaches is partly stochastic.

Collectives

Social cockroaches form aggregations. This group formation is spontaneous (i.e., the aggregations are the result of individual behavioral rules, there is no „higher force“ ruling cockroaches to aggregate).

Observation

We observe the distribution of sociality among cockroaches.

4.2.5 Initialization

State variables have deterministic initial values (written in Table 4.1). These values have been chosen arbitrarily. In the case of state variables representing the state of real nature (e.g., how much energy do cockroaches burn by sitting per unit time), empirical values are unknown to our knowledge. We have aimed for such values, which lead to reasonably plausibly looking behavior.

4.2.6 Input data

The model does not use input data to represent time-varying processes.

4.2.7 Submodels

Food addition

In this phase, representing the phase 1 of 4.2.3, an amount of food equal to food growth environment constant is added to all patches in the environment. This model has been chosen because it is easily understood and it should not confuse us when analyzing results of our experiments.

This food represents generic “dirt” that cockroaches are able to eat and they do not have many competitors for it in the nature.

Pheromone dispersion

This phase represents the phase 2 of 4.2.3. See 3.2.7 for its description.

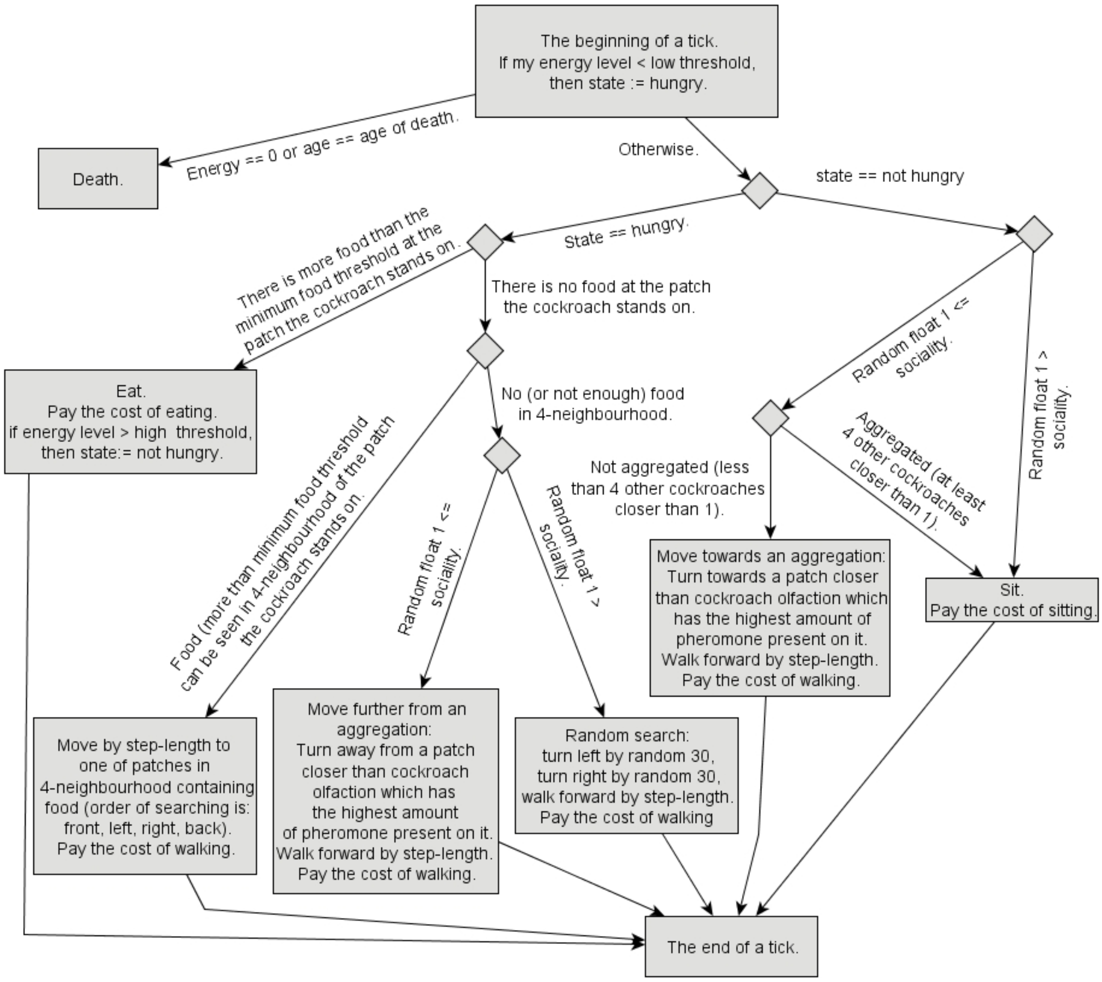

Figure 4.1: The diagram describing cockroach action-selection rules.

Pheromone addition

This phase represents the phase 3 of 4.2.3. See 3.2.7 for its description.

Cockroach movement

This phase represents the phase 4 of 4.2.3.The action-selection rules of cockroaches, including all rules of movement, are described in Figure 4.1.

What does it mean to decide whether to behave socially or not? The sociality is an integer ranging from 0 to 10; at the moment of decision, random 10 is generated and if it is lesser than the cockroach's sociality, the cockroach behaves socially. Otherwise, the cockroach behaves asocially.

We define "to be in an aggregation" as to be in such a position that at least 4 other cockroaches are closer than 1[6]. When a social cockroach is aggregated and not hungry, he sits and rests.

All actions (walking, sitting, eating) cost the amount of energy specified in Table 4.1.

[6]Actually, we do not know whether it is "closer than 1" or "closer than 1 or in distance 1"; it depends on internal NetLogo implementation. However, as we operate in float coordinates, the difference should be nonessential.

Cockroach eating

If a hungry cockroach is on a patch with enough food (more than the `minimum food threshold` constant, i.e., more than 0.3), he eats. The amount of food eaten is:

$$F_e = min\{F_p, \frac{e_{max} - e_{cur}}{e_f}\}$$

where F_e is the amount of food eaten, F_p is the amount of food currently present at the patch, e_{max} is the `maximum cockroach energy`, e_{cur} is the `energy` of given cockroach, e_f is the `energy from food` constant. The fraction $\frac{e_{max}-e_{cur}}{e_f}$ represents the maximum amount of food a cockroach is able to eat to refill his energy completely.

Reproduction

This phase represents the phase 5 of 4.2.3. The probability of reproduction of a cockroach is:

$$p_{rep} = \frac{e}{10000}$$

where p_{rep} is the probability of reproduction and e is the `energy` of the cockroach. This way, stronger cockroaches (having more energy) have better chance of reproduction, which represents better chances in competition for sexual partners. If a cockroach does reproduce, he splits his energy into two halves: one is kept, one is given to the newborn cockroach[7]. The newborn cockroach is a copy of the parent, except the value of `sociality`, which may be decreased by 1, increased by 1 or kept the same (all possibilities have the same probability). The sociality may never be lower than 0 or higher than 10; In the case of `sociality` of the child becoming -1, 0 is used instead; in the case of `sociality` of the child becoming 11, 10 is used instead.

Aging

This phase represents the phase 6 of 4.2.3. Every tick, 1 is added to `age` of all living cockroaches. Those with age equal to `maximum age` will die in the next tick.

Pheromone evaporation

This phase represents the phase 7 of 4.2.3. See 3.2.7 for its description.

4.3 Model variants

Hypotheses 4.1.2 and 4.1.3 are[8] tested on slightly different models, both extending the basic model 2.0 described in the ODD protocol. Those extensions are described in this section.

[7]This 50:50 ratio has been chosen arbitrarily, we do not know biologically plausible values.
[8]Hypotheses 4.1.1 is tested by Model 2.0.

4.3.1 Model 2.1

This model is used to test the hypothesis 4.1.2. In the basic model, dead cockroaches simply vanished. In this extended model, dead cockroaches turn to food instead. There is a new variable introduced: `total energy gained`. It represents how much energy has a cockroach gained in his life, the initial value being 100 (and it is always raised when the cockroach eats). When cockroaches reproduce, the newly sprouted cockroaches set it to the amount of energy he gains from his parent.

Also, the state constant `energy wasted` has been introduced. It determines, how much food eaten by a cockroach is burned and how much contributes to his body mass. The higher this value is, the larger amount is burnt (therefore the value of cockroach corpses will be generally lower).

The value of the corpse of a cockroach is:

$$F_l = \frac{e_t}{e_w \cdot e_f}$$

where F_l is the amount of food added to the patch where the cockroach died, e_t `total energy gained` of the given cockroach, e_w is `energy wasted` and e_f is `energy from food` (energy units must be converted to food units). The value of `energy wasted` $= 2$[9] has been chosen after discussion with Daniel Frynta and Zuzana Varadínová, it means that half of the food a cockroach has eaten in his life was burned and the other half transformed into body mass which may be eaten by other cockroaches after the cockroach dies.

Let us make an important remark, when one would modify our model, a care has to be taken to prevent "perpetuum mobile" from appearing in the model: If, for example, a cockroach has been converted to $\frac{\texttt{total energy gained}}{\texttt{energy from food}}$ units of food (i.e., two times the current amount), all the food he has eaten would be returned to the system. Therefore, no food would be removed from the system permanently. However, every tick, food is added to the system. When there is food added to the system and no food removed (burnt) permanently, the amount of food grows infinitely, which leads to infinite growth of cockroach population. This is definitely not a plausible behavior.

4.3.2 Model 2.2

This model is used to test the hypothesis 4.1.3. It extends the basic model (not Model 2.1), so it is an alternative to Model 2.1. In this extension, cockroaches leave feces behind them. After finishing the movement phase, cockroaches add small amount of food to the patch they are standing on. The amount is the value of newly introduced environment constant `feces-value`, which is 0.05 (i.e., 0.25 units of energy, which is $\frac{1}{2}$ of cost paid for sitting).

4.4 Experiment description

Although we have formulated three hypotheses and created three models, there is technically only one experiment ran with all three models: 20 cockroaches are

[9]When we tried to set it to 3, i.e., less valuable, results were qualitatively the same.

created. Then, the population is allowed to live and evolve for 50000 ticks (i.e., at least 200 generations)[10]. In the 50001st tick, the distribution of sociality among cockroaches is collected (this distribution is the result of the experiment).

The experiment has been ran with four different initial values of `food growth` parameter: 0.01, 0.04, 0.99, 0.1. This is to test how does the sociality evolve in environments with low, middle and high amount of food.

The value 0.1 is an edge value: when such amount of food is added to all the patches in the environment, it is enough to cover the energy cost of sitting of cockroaches. Strange behavior may emerge, we just wanted to see how cockroaches would behave under such circumstances.

For better statistical credibility, all simulation runs with different parameter configurations have been repeated 100 times.

We will further use the following terminology:

- Experiment 2.0: The described experiment ran using Model 2.0; used to test the hypothesis 4.1.1.
- Experiment 2.1: The described experiment ran using Model 2.1; used to test the hypothesis 4.1.2.
- Experiment 2.2: The described experiment ran using Model 2.2; used to test the hypothesis 4.1.3.

4.5 Results

As there are three separate hypotheses to be tested, this section is subdivided into three parts, each discussing an analysis of a single experiment. See Figure 4.2 for an example of how may the evolution of sociality look (this example has been taken from Model 2.1, with `food growth` = 0.04).

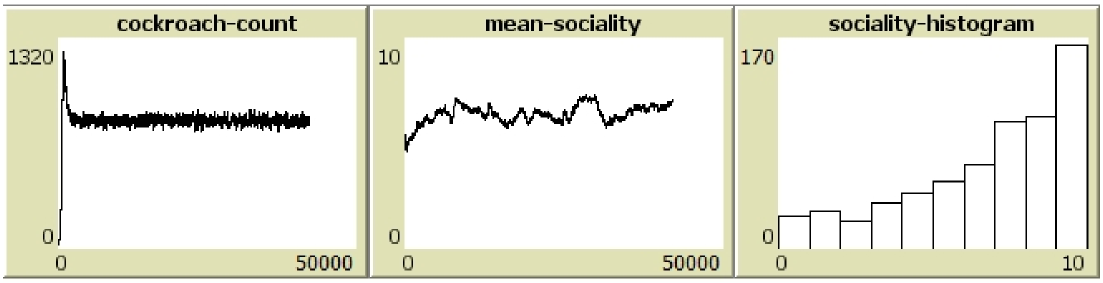

Figure 4.2: An example curve depicting the evolution of sociality among cockroaches in Model 2.1. The initial "bump" in the size of population is caused by the environment not being initialized in its "natural" state.

4.5.1 The results of Experiment 2.0

The distribution and means of the `sociality` at the end of the experiment (see Figure 4.4 and Table 4.2) clearly show the prevalence of low sociality. Indeed,

[10]To make sure that such a state is stable, we ran the model for 1000000 ticks four times and in all four cases, the model was stable from circa 15000th tick.

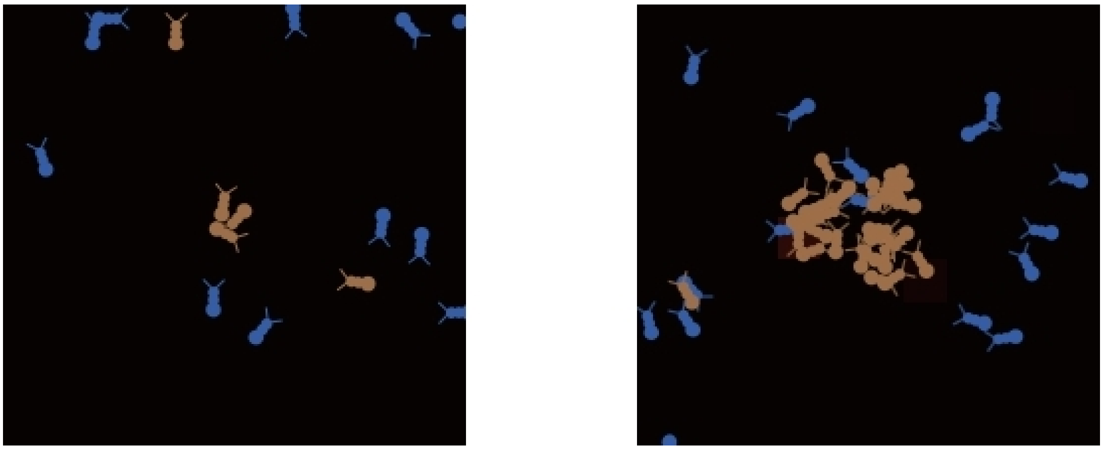

Figure 4.3: The left screenshot is a visualization of a small aggregation formed by cockroaches with low `sociality`. The right screenshot is a visualization of larger aggregation formed cockroaches with high `sociality`. Let us note that brown bugs are non-hungry cockroaches and blue bugs are hungry cockroaches.

`food growth`	mean `sociality`	variation of `sociality`
0.01	2.085652	4.107399
0.04	1.907567	3.720182
0.099	2.470747	5.998973
0.1	2.491685	6.032909

Table 4.2: The table of mean sociality of cockroaches in the experiment 2.0 (it is counted from all the 100 runs of the experiment).

when we have observed the behavior of the model visually, aggregations were small and short-lived (see Figure 4.3, left). Therefore, we have to reject the hypothesis 4.1.1, social cockroaches were beaten by asocial cockroaches; simple random food-searching strategy is more efficient than the strategy described in the hypothesis 4.1.1 formulation.

Higher `food growth` facilitates slightly higher average sociality, but the difference is rather small indeed. With lower values of `food growth`, there is much higher variance of the `sociality` distribution. The main reason is that lesser amount of food leads to less cockroaches alive at a moment. Smaller population of cockroaches is less stable, i.e., there are relatively larger oscillations in the population size; this leads to larger variance.

Additional research

Further analysis of the model shows that the hypothesis 4.1.1 is not completely nonsensical. The first possibility for such a low overall sociality after the experiment is, that the use of chemical signal is downright misleading when cockroaches try to find food. An alternative explanation is, that even though it is more effective to go against the chemical gradient than to search for food randomly, the price for returning to the aggregation is too high (a cockroach has to move to get back to an aggregation, which is much more energetically expensive than if he sat). To resolve this question, we have made the following modification of our

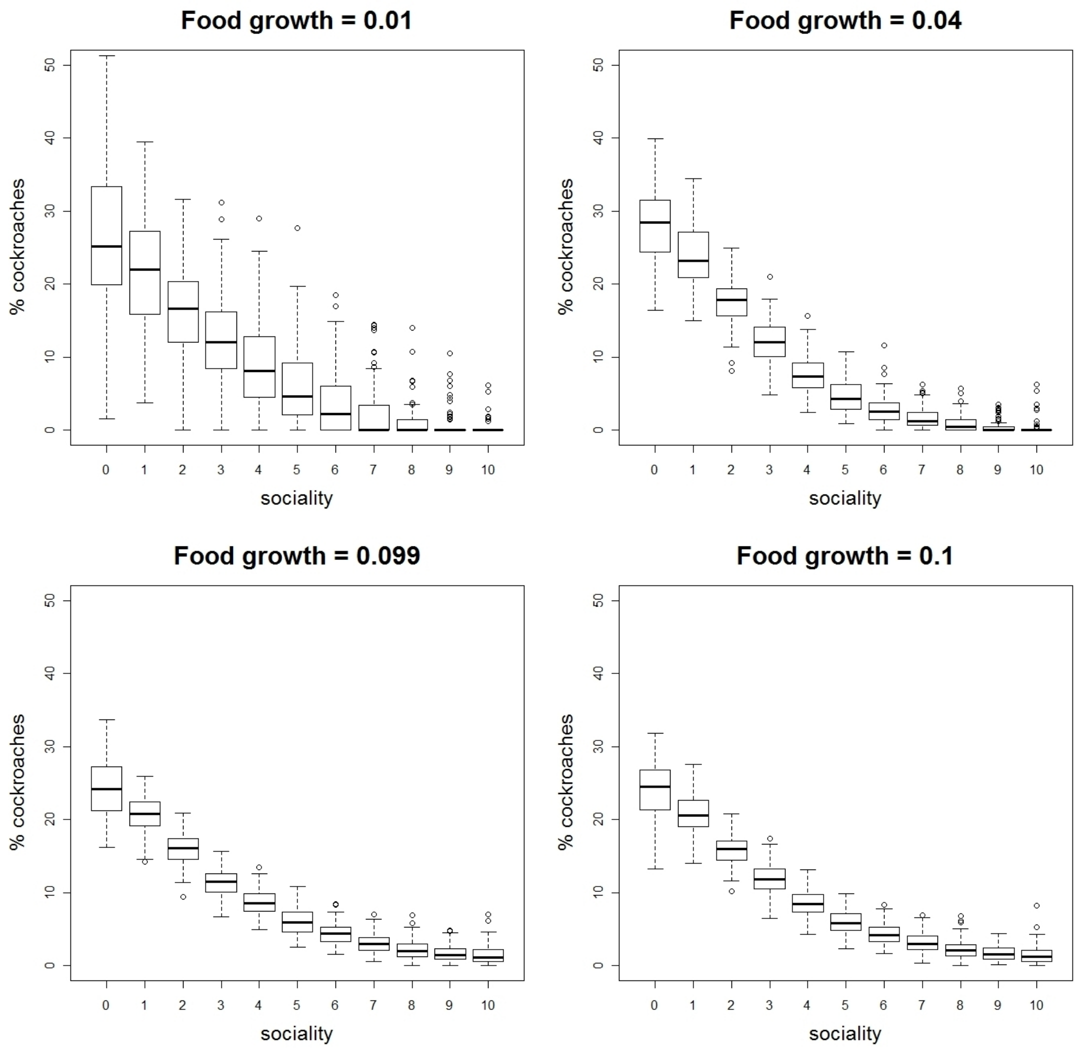

Figure 4.4: The histogram of sociality of cockroaches after 50 000 ticks in Model 2.0. The cockroach sociality is on the x axis, the percentage of cockroaches having it is on the y axis.

model:

The social behavior has been slightly redefined: when a cockroach is hungry, he tries to find food randomly (not using the chemical signal), when not hungry, he returns to an aggregation (the same behavior as in the former model). This way, he still pays price for his sociality (burns energy when returning to an aggregation, it is more expensive than if he sat still), but he should not be able to use the merits an aggregation offers him (i.e., he won't utilize the chemical signal when trying to find food). We have ran the same experiment with this updated model, as with the former one. The resulting average `sociality` was noticeably lower. Therefore, the movement against the chemical gradient in case of hunger confers an advantage (the cockroach is able to find food more easily), but the price paid for it (the energy price of returning to the aggregation) is too high.

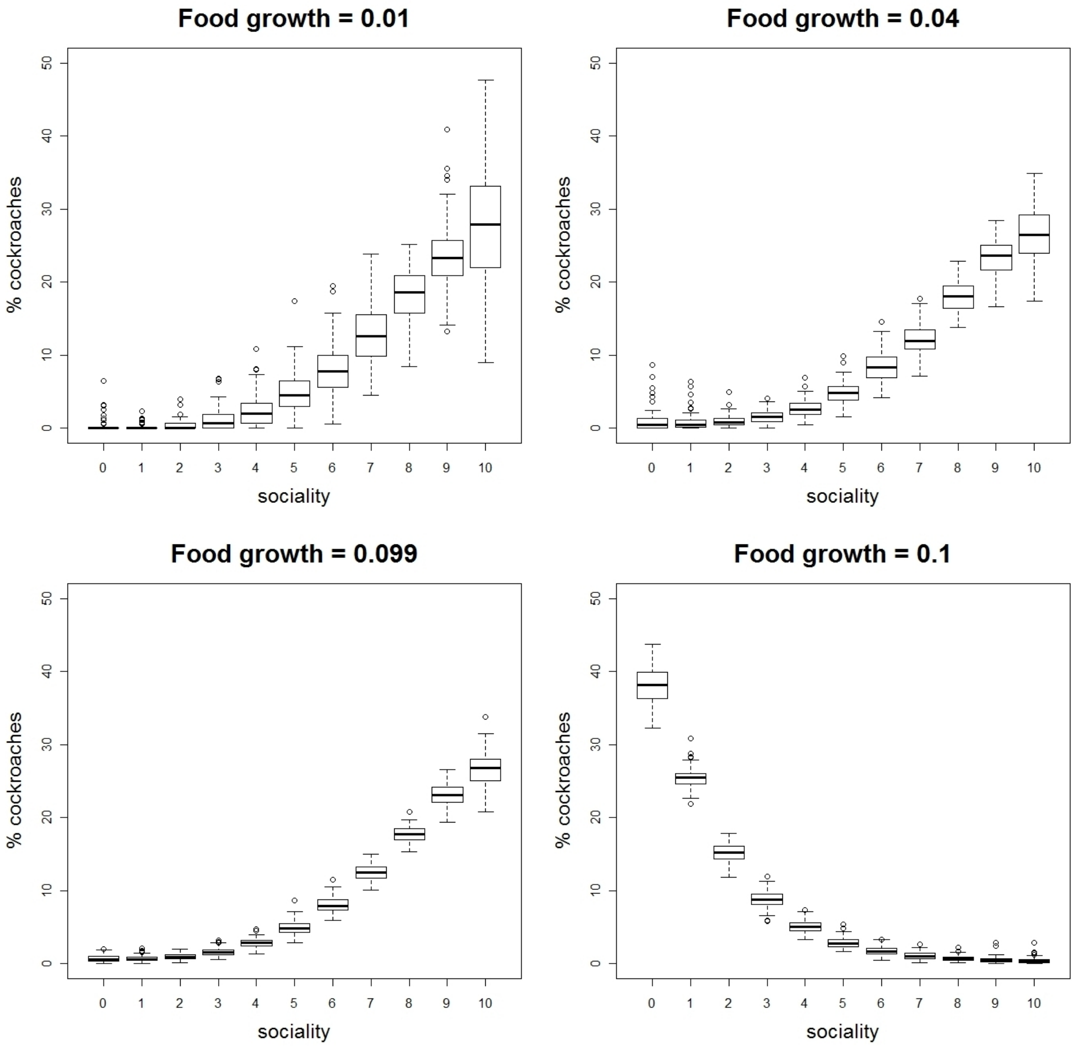

Figure 4.5: The histogram of sociality of cockroaches after 50 000 ticks in Model 2.1. The cockroach sociality is on the x axis, the percentage of cockroaches having it is on the y axis.

4.5.2 The results of Experiment 2.1

Except in the extreme case of the `food growth` = 0.1, high sociality clearly prevails when cockroaches are necrocannibals, see Figure 4.5 and Table 4.3. As a result of such a high sociality, several large aggregations were formed and they lasted for a very long time, see the right part of 4.3. Therefore, the hypothesis 4.1.2 is supported by our data.

In the extreme case of `food growth`, the aggregation was not formed, the distribution of cockroaches in the universe was rather homogeneous. Why was that so? As we have said, with such a high `food growth` (0.1), the growth of food is high enough to cover the energy cost of sitting. Therefore, the ideal situation for cockroaches is when there is a single cockroach on a single patch only. Such a cockroach is well-fed and does not need to aggregate. The behavior of dispersing themselves in the environment is definitely not social and indeed, when we have observed the model visually, most cockroaches did not move at all (only "surplus" cockroaches competing with sitting cockroaches). However, let us note that such a high value of `food growth` is not plausible as there is rarely enough food in the nature that the cockroaches could sit and wait for the food to come.

Additional research

We have shown that incorporation of the necrocannibalism leads to the evolution of a high sociality. But why? How exactly does it benefit cockroaches? We have formulated several hypotheses and tested them:

1. *As cockroach corpses turn to food and stay in the aggregation, many social cockroaches can find food easily (it is in the aggregation), therefore they do not have to move as much as asocial cockroaches. Therefore, social cockroaches spend less energy on walking than asocial cockroaches, which leads to higher average* `energy` *and higher rate of survival.*

   We rejected this hypothesis; when we measured the amount of walking and sitting moves, asocial cockroaches walked less than social cockroaches and sat more.

2. *We have observed that social cockroaches have a larger average* `energy` *than asocial cockroaches. As the probability of reproduction depends on the the value of* `energy`*, the cockroaches with the higher level of it will reproduce more often. Therefore, social cockroaches should reproduce more than asocial cockroaches, which could be an explanation.*

   We rejected this hypothesis; when we removed the dependence of reproduction probability on the level of `energy` (i.e., all cockroaches had the same probability of reproduction), the prevalent sociality was still very high. If the tested hypothesis has been true, social cockroaches would lose their advantage (being able to reproduce more) and evolved `sociality` would be low.

3. *It could be true that the food-searching strategy of social cockroaches is more effective when there are several patches with high amounts of food (corpses), instead of all patches having a small amount of food.*

   This hypothesis has not been supported by our data. We have used the basic model 2.0 and extended it. The food addition has been changed slightly: in addition to the normal food addition mechanism, large amount of food was sometimes added to several patches (all patches had the same probability of being chosen). This phenomenon has been created to emulate dead bodies of cockroaches (since we extended Model 2.0, there is no necrocannibalism).

`food growth`	mean `sociality`	variation of `sociality`
0.01	8.142344	3.325038
0.04	7.955582	4.342325
0.099	7.970005	4.205119
0.1	1.500870	3.425021

Table 4.3: The table of mean sociality of cockroaches in the experiment 2.1 (it is counted from all the 100 runs of the experiment).

If the given hypothesis was true, high sociality would evolve in such a model (i.e., with no corpses, with their emulation only). When we ran experiments with this model, the resulting sociality was always very low.

4. *As there is a higher concentration of cockroaches in an aggregation than outside, there could be higher concentration of dead cockroaches as well. Such a concentration would lead to more food being in aggregations than outside, which is why it would be advantageous to be social: social cockroaches would have access to more food than asocial ones.*

   Our results suggest that this hypothesis is true. When we measured the average amount of food from corpses on patches in aggregations, it was 12-20% higher than outside aggregations. We believe that this larger amount of food leads to less frequent death of hunger of social cockroaches than asocial ones. However, it would be good to verify this belief, it is a rather important future work.

4.5.3 The results of Experiment 2.2

The results of this experiment (see Figure 4.6 and Table 4.4) clearly show the prevalence of low sociality. As a result, the hypothesis 4.1.3 has not been supported. With lower values of `food growth`, the difference from the results of experiment 2.0 is very small. With higher values of `food growth`, the resulting mean `sociality` is higher. The reason is probably that with such a high values of `food growth`, cockroaches do not move as much as when there is little food. Therefore, an aggregation of mostly sitting cockroaches produces feces which can be utilized by other members of the aggregation immediately. When cockroaches move a lot from an aggregation, their feces are spread in the environment and it are not as easily edible by other members of the given aggregation.

`food growth`	mean `sociality`	variation of `sociality`
0.01	2.279228	4.586424
0.04	1.884497	3.487311
0.099	3.411576	8.485322
0.1	3.380743	8.295087

Table 4.4: The table of mean sociality of cockroaches in the experiment 2.2 (it is counted from all the 100 runs of the experiment).

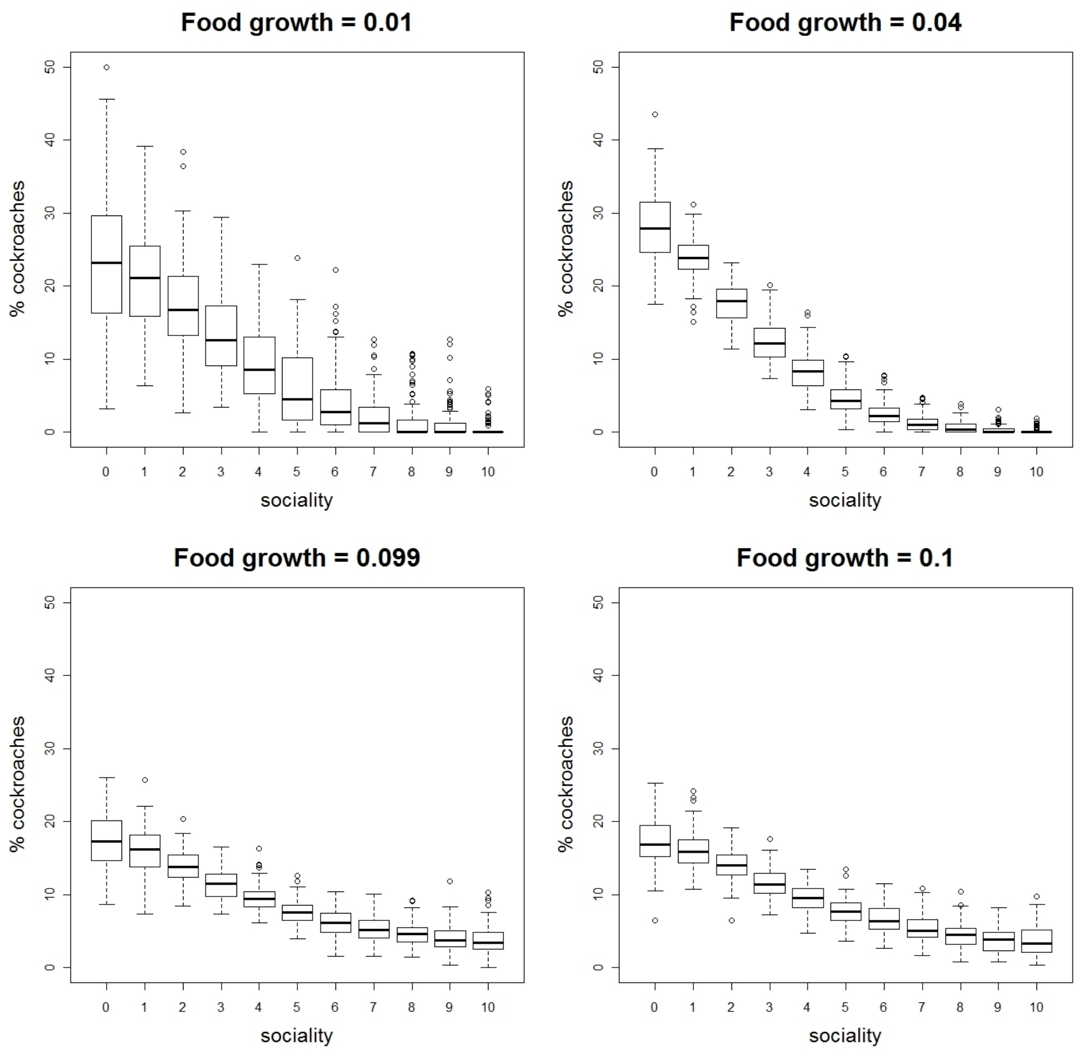

Figure 4.6: The histogram of sociality of cockroaches after 50 000 ticks in Model 2.2. The cockroach sociality is on the x axis, the percentage of cockroaches having it is on the y axis.

4.6 Discussion

In this chapter we have formulated and tested three hypotheses which could explain why is aggregation evolutionarily advantageous: on food-searching strategy of cockroaches, on effective use of corpses via necrocannibalism and on effective use of feces via coprophagy. From these hypotheses, only the second has been supported by our data, other two hypotheses have not been supported.

Our results show the importance of cockroach necrocannibalism. Our interpretation of the cockroach necrocannibalism is that cockroaches simply bring food to their aggregation in this way. Ants and some other insects carry food to the aggregation on their back and/or in mandibles, cockroaches do not or not too much (Daniel Frynta, personal communication, 18.5.2011). When a cockroach eats food outside an aggregation, returns to the aggregation, dies there and is eaten, food from outside is brought into the aggregation in a way. We consider this result particularly important, as in our model, food from corpses was only universal food. In reality though, a corpse contains important proteins and is probably even more valuable than food usually found by cockroaches. If necrocannibalism was a way of obtaining nutrients rarely found in other food, it would be even better reason to aggregate. However, we have shown that even without the added value of rare nutrients, necrocannibalism leads to aggregation formation.

In nature, a cockroach even does not have to die, because cockroaches leave an exuvia after moulting. Such an exuvia is rich in proteins and chitin and is very valuable to other cockroaches [8, p. 72]. Cockroach often moult in an aggregation[11] – thus bringing proteins and chitin into aggregation to be shared.

Although the incorporation of coprophagy to our model did not lead to social behavior and aggregation formation, it does not mean that coprophagy is not important in nature. Maybe our model would behave differently if, when cockroaches reproduce, would the parent keep 80% of his energy and the child would get only 20%. Also, we have not included predation and defense against it in this model. In nature, cockroach nymphs need proteins to grow, but it may be difficult and dangerous for them to obtain them. When fed by parents' feces, they can be much safer and more of them can survive. Our model has not been created with these thoughts in mind, it was rather general[12]. Creating and analyzing a model specialized at cockroach coprophagy could be an interesting future project.

We have shown the importance of necrocannibalism in cockroaches. Let us realize that if cockroaches were aggressive and killed one another occasionally, there would be even more corpses to be eaten. But more cockroaches would die too (in extremal case, whole aggregation could "eat itself"). Actually, in reality, cockroaches sometimes do kill one another. The next chapter concentrates on the phenomenon of cockroach aggressivity and tries to explain why it could be advantageous to cockroaches.

[11] Daniel Frynta, personal communication, 21.5.2011; the reason is probably the predation pressure outside an aggregation.

[12] I.e., food from feces was represented by generic food in our model; in nature, it may be more valuable as it contains proteins. Also, we have not included predation in the model.

5. Model line 5: Cockroach aggressivity

Cockroaches sometimes attack and eat one another in nature [8, p. 71]. How is this aggressivity moderated so that cockroaches do not die out? Why do cockroaches aggregate, even though they may be killed in an aggregation?

The basic model 5.0[1] of this model line is an extension of Model 2.1, i.e., we will presume the existence of necrocannibalism among cockroaches. The modifications of Model 2.1 were rather large and our hypotheses tested on the extension are quite different from hypotheses tested by Model 2.1. For those reasons, we have created a separate line of models purely to test and observe the phenomenon of cockroach aggressivity.

In this model, we wanted to take an exploratory approach: to create a model of social aggressive cockroaches and observe it; we did not have any hypotheses before. Therefore, following hypotheses were created during these observations.

5.1 Hypotheses formulation

5.1.1 Higher energetic efficiency

In nature, cockroaches sometimes walk, sometimes they sit. It is natural to expect that when a cockroach sits, he burns less energy per unit of time than when he walks. We propose that when cockroaches kill one another "reasonably", i.e., they do not extinguish themselves, more food (from dead cockroaches) will be concentrated in aggregations, therefore cockroaches will have to leave the aggregation less often to find food outside, thus burning less energy. When an aggregation as one entity has more energy, it may produce and keep more cockroaches.

In the analysis of Model 2.1, we proposed an idea that cockroaches bring food to an aggregation in their bodies and when they die, aggregated cockroaches do not have to go outside the aggregation, they can eat the corpse instead. The idea of aggressivity furthers this idea, even more food should be present in aggregations.

Hypothesis summary: We propose that reasonably aggressive cockroaches do not burn as much energy as nonaggressive cockroaches; this results in higher number of sustainable cockroaches in the environment.

5.1.2 Invasion protection

When testing how advantageous a strategy of a population is, it is important to test the invasibility of such population. In other words, it is important to test the population against competing populations (with different behavior) and see who wins, i.e., which population extinguishes the other one. It is also possible that both populations will survive and that such a state will be stable. We expect

[1]Model lines 3 and 4 exist too, but we could not include them in this thesis due to spatial limitations. Results of these models were not important. Nevertheless, as these two model lines exist, we held to our internal numbering of model lines, thus keeping the model line concerning cockroach aggregation as Model line 5.

that reasonably aggressive social cockroaches will win against nonaggressive social cockroaches, as well as against asocial cockroaches (being reasonably aggressive or not aggressive at all). We expect that nonaggressive social cockroaches will win against nonaggressive asocial cockroaches[2], but will lose against reasonably aggressive cockroaches.

Hypothesis summary: We propose that a population of reasonably aggressive cockroaches is not invasible by nonaggressive, nor asocial cockroaches, while a population of nonaggressive cockroaches is invasible by aggressive cockroaches.

5.1.3 Easier survival of periods with no food

Even though real cockroaches are not too picky when it comes to their choice of food, a period of hunger may strike them. When no food is added to their habitat, nonaggressive cockroaches will search further from their home aggregation and when they die (of hunger or of age), their corpse will be difficult to find (and eat) for other cockroaches. As a result, most cockroaches will be walking (and burning a lot of energy) and the positive effect of necrocannibalism will be weak.

On the other hand, when no food is added to a habitat of aggressive cockroaches, they will start eating one another in the aggregation (therefore burning little energy as most of them will sit). This may, of course, lead to complete extinction if the food is not added for a very long time (note that in such a case, nonaggressive cockroaches would die of hunger too), but if food starts to be added into the system again, the aggregation of aggressive cockroaches may begin harvesting it again. The crucial part is that when no food is added, aggressive cockroaches mostly sit (if they become hungry, they kill another cockroach), therefore they burn little energy (much less than nonaggressive cockroaches).

In slightly other words, when no food is added to the system, all food (grown before food ceased to be added) will be eaten eventually. After it happens, cockroach corpses will be the only source of food. If cockroaches are aggressive, most corpses will be in (or nearby) aggregations. Such corpses are easy to find and searching cockroaches do not have to burn too much energy to find such corpses. On the other hand, not aggressive cockroaches will be running in the environment, searching for food and they may die far from aggregations. As a result, it will be more difficult and more expensive for other cockroaches to find them and eat them.

This whole thinking is based on the thought that attacking is not overly expensive (in means of energy). If it has been too expensive, the benefit of more sitting and less walking, thus burning less energy, would be wasted by expensive attacks and aggressivity would not be an advantage.

Hypothesis summary: We propose that aggressive cockroaches will survive longer periods of time when no food is added to the environment.

5.1.4 Natural evolution and higher sociality facilitation

We propose that if we allow cockroaches to evolve their sociality and aggressivity at the same time, a state similar to the natural state could evolve, i.e., high sociality and reasonable aggressivity [8], would be dominant.

[2] This is what Experiment 2.1 in 4.5.2 has shown.

5.2 Model description

The basic model of the model line 5 is described here. It is numbered 5.0. The variants of this basic model are described in the next section.

5.2.1 The purpose

The purpose of this model is to test the hypotheses 5.1.1 and 5.1.2. The model will be extended to test the other two hypotheses too.

5.2.2 Entities, state variables and scales

There is only one breed of agents inhabiting the environment – cockroaches.

Environment constants are described in Table 5.1. Other state variables are described in Table 5.2. We suggest reading 4.2.2 too as purposes of certain state variables are explained there.

As opposed to Model 2.1, cockroaches in this model live longer, have larger capacity of energy and have modified low and high energy threshold. The cockroach life has been prolonged to have larger variation of cockroach age (as when we designed the model, we have already known that cockroach ability to fight would depend, directly or indirectly, on their age). Changes of thresholds were made because of a belief they will lead to more "reasonable" behavior of cockroaches: with `low threshold` = 30 in model 2.1, cockroaches too often died searching for food, when it was not that distant (or because other cockroaches being on the same patch acted before them and ate all the food on the given patch). They became hungry when their `energy` got below 30, which gave them 15 ticks to find food which seems to be too short time. `High threshold` has been raised so that cockroaches which find food outside an aggregation and return still have enough energy to sit and rest for some time[3].

`Sociality` of cockroaches has been changed slightly, its value is not an integer integer of 0–10, it is a float of 0–1 instead. The meaning is the same though. `Sociality` = 0 means that a cockroach is never social, `sociality` = 1 means that a cockroach is always social. This change of scale was done simply so that `sociality` determines the probability of being social directly.

Compared to Model 2.1, we have introduced a new constant `maximum eating`. When we visually observed and evaluated Model 2.1, we realized that it is not very realistic that a cockroach would swallow a dead cockroach in a single tick and no other cockroaches would have their share (in nature, more cockroaches would probably feast on the corpse together). Since food from dead cockroaches is crucial in this model line, we have limited the amount of food a cockroach may eat in a single tick.

When designing costs of various actions, we did not know exactly how expensive should attacking be (according to our knowledge, no one has measured the energy cost of cockroach actions in real nature). We set it rather expensive as

[3]Let us note though that when we were experimenting with the model outside this research, we came to the conclusion that the model is not particularly sensitive to values of these changed variables. It could be a future work to test it systematically

real cockroaches mostly attack cockroaches which are easy to kill (Daniel Frynta, personal communication, 18.5.2011)[4].

When deciding whether to attack or not, a cockroach uses his `aggressivity`, which is, similarly to `sociality`, a float of 0–1. There is a global constant `social aggressivity` which determines `aggressivity` of cockroaches. In several extending models, it is not used anymore as `aggressivity` of cockroaches is inherited and mutated.

5.2.3 Process overview and scheduling

Within every tick, several phases are processed in the following (given) order:

1. Food is added to the environment.
2. The chemical pheromone disperses in the environment.
3. Cockroaches add certain amount of the pheromone to the environment.
4. Cockroaches act (they move, eat and attack in this phase).
5. Cockroaches reproduce.
6. Cockroaches age.
7. A part of the chemical pheromone evaporates.

The order of cockroaches in which they act in every tick is random.

5.2.4 Design concepts

Emergence

We expect that interesting results concerning consequences of cockroach aggressivity may emerge. Also, because of the chosen model of cockroach behavior, aggregation formation is an expected phenomenon.

Adaptation

Modelled cockroaches are not adaptive in their life, their `sociality` may change between generations though.

Objectives

The objective of modelled cockroaches is to have enough food and to survive. The objective of social cockroaches is to be near other cockroaches. When these objectives are fulfilled, a cockroach sits and waits[5]. Subobjectives of cockroaches are mentioned in the section 5.2.7 in the part about cockroach action.

[4]When experimenting with the model, we tried even `attack cost` = 10, our results were qualitatively unchanged.

[5]This means that well-eaten cockroaches do not explore the environment; this presumption does not have to be necessarily true in nature.

Name	Description	IV
`universe width`	How wide (in patches) is the environment.	40
`universe height`	How high (in patches) is the environment.	40
`pheromone dispersion rate`	Determines how much pheromone disperses every tick.	20
`pheromone evaporation rate`	Determines how much pheromone evaporates every tick.	10
`pheromone added`	How much pheromone does a single cockroach add to the environment in a single tick.	10
`cockroach olfaction`	The range in which are cockroaches able to detect the concentration of the pheromone.	5
`energy from food`	How much energy is gained from one unit of food.	5
`maximum eating`	How many units of food may a cockroach eat in a tick.	20
`basic reproduction probability.`	The basic probability that a cockroach will reproduce. It is further modulated by the given cockroach's strength.	0.001
`food growth probability`	The probability that 2 units of food will appear on a patch.	0.004
`maximum energy level`	The maximum amount of energy a cockroach may have.	200
`low energy threshold`	When the value of `energy level` is under this threshold, a cockroach becomes hungry.	50
`high energy threshold`	When the value of `energy level` is above this threshold, a cockroach becomes not hungry.	180
`minimum food threshold`	When the amount of food on a patch is lesser than this a cockroach will not eat it.	0.3
`step length`	How far does a cockroach walk in a single move.	1
`maximum age`	The age when a cockroach dies of age.	1000
`cost of sitting`	How much energy a cockroach burns when he sits.	0.5
`cost of eating`	How much energy a cockroach burns when he eats.	1
`cost of walking`	How much energy a cockroach burns when he walks.	2
`cost of attack`	How much energy a cockroach burns when he attacks.	5
`energy wasted`	Determines how much energy is burnt by a cockroach and how much contributes to his growth. See 4.3.1 for further description.	2

Table 5.1: Initial values (IVs) of environment constants are written in this table.

Name	Type	Description	IV
`number of cockroaches`	e. v.	How many cockroaches are in the environment	20
`social aggressivity`	e. p.	The initial value of `aggressivity` of cockroaches.	-
`food amount`	p. v.	How much food is on a patch.	0
`pheromone amount`	p. v.	How much pheromone is on a patch.	0
`total energy gained`	c. v.	How much energy has a cockroach gained in his life (this represents his size and strength).	200
`energy level`	c. v.	How much energy a cockroach has.	200
`aggressivity`	c. v.	The current aggressivity of a cockroach (the probability that a cockroach will behave aggressively).	[6]
`sociality`	c. v.	The current sociality of a cockroach (the probability that a cockroach will behave socially).	[7]
`age`	c. v.	How old a cockroach is.	0
`state`	c. v.	Whether the cockroach is hungry (1) or not (0)	0

Table 5.2: Initial values (IVs) of patch and cockroach variables are written in this table. The Type determines whether the variable belongs to patches (p.) or cockroaches (c.).

Sensing

Modelled cockroaches sense the pheromone signal in their vicinity. They are able to know how much pheromone is in a circle of radius `cockroach olfaction` around them[8]. Cockroaches can also detect the amount of food on the patch they are standing on and in their 4-neigbourhood. Cockroaches are able to determine the strength of cockroaches in the vicinity. Strength is a cockroach variable dependent on the value `total energy gained`; as it is dependent, it is not mentioned in the table of cockroach variables)

Interaction

Cockroaches are capabble of attacking and killing one another. They indirectly interact with one another via their pheromone signal.

[6] the initial value is equal to `social aggressivity`. In Model 5.3 and 5.3.1, it is evolved. In other models, it is always equal to `social aggressivity`.

[7] the initial value is equal to random float 1. We have changed the scale of `sociality` to 0-1 (float) instead of 0-10 (integer) used in Model 2. The meaning is the same though, 0=asocial, 1=fully social.

[8] See 4.2.2 for discussion of this mechanism.

Stochasticity

The stochasticity is a part of the model. Cockroach decisions whether to attack another cockroach or not are modelled stochastically, as well as the cockroach reproduction. Whether a cockroach behaves socially or asocially is stochastic too.

Collectives

Modelled cockroaches form aggregations. This aggregation formation is a result of individual behavior, it is not ruled by a higher force.

Observation

We observe impacts of various levels of aggression on the cockroach population: its size, healthiness (the total amount of energy in all cockroaches) and its food collection efficiency (how much energy is burned on various moves).

5.2.5 Initialization

State variables have deterministic initial values (written in Table 5.1 and Table 5.2). These values have been chosen arbitrarily. In the case of state variables representing the state of real nature (e.g., how much energy do cockroaches burn by sitting per unit time), empirical values are unknown to our knowledge. We have aimed for such values, which lead to reasonably plausibly looking behavior.

5.2.6 Input data

The model does not use input data to represent time-varying processes.

5.2.7 Submodels

Food addition

This phase represents the phase 1 of 5.2.3. Every tick, on every patch, 2 units of food[9] are added with a probability `food growth probability` (random float 1 is generated, if smaller than `food growth probability`, the food is added).

Pheromone dispersion

This phase represents the phase 2 of 5.2.3. See 3.2.7 for its description. Note though, that we have chosen a slightly different value of `pheromone dispersion` for this model. We believed it would lead to slightly more plausibly looking behavior than with the old value; that there would be larger aggregations formed. However, when we evaluated the finished model, we came to the conclusion that we could have used the old value too, the difference is little if any. There could be a lot of future work done on research of plausible behavior of the aggregation pheromone.

[9] i.e., 10 units of energy

Pheromone addition

This phase represents the phase 3 of 5.2.3. See 3.2.7 for its description.

Cockroach action

This phase represents the phase 4 of 5.2.3. The rules of cockroach behavior are described in Figure 5.1. As it was not possible to fit all the rules into a single diagram, we have used a main diagram which, at two places, points to other diagrams.

When there is "random float 1 < `sociality`" in the diagrams, it means that a cockroach is "deciding" whether he will behave socially or not (`sociality` is the probability of behaving socially). It is obvious that a cockroach with sociality = 1 will always behave socially. "Random float 1 < `aggressivity`" is, similarly, a decision whether to behave aggressively (attack another cockroach) or not.

Compared to Model 2.1, we have slightly redefined when a cockroach thinks that he is aggregated. In Model 2.1, he was aggregated when there were at least four other cockroaches closer than 1. This has lead to formation of very small and tightly packed aggregations. To make aggregations spread in space a bit, we now say that a cockroach thinks he is aggregated when there are at least 9 other cockroaches closer than 2.

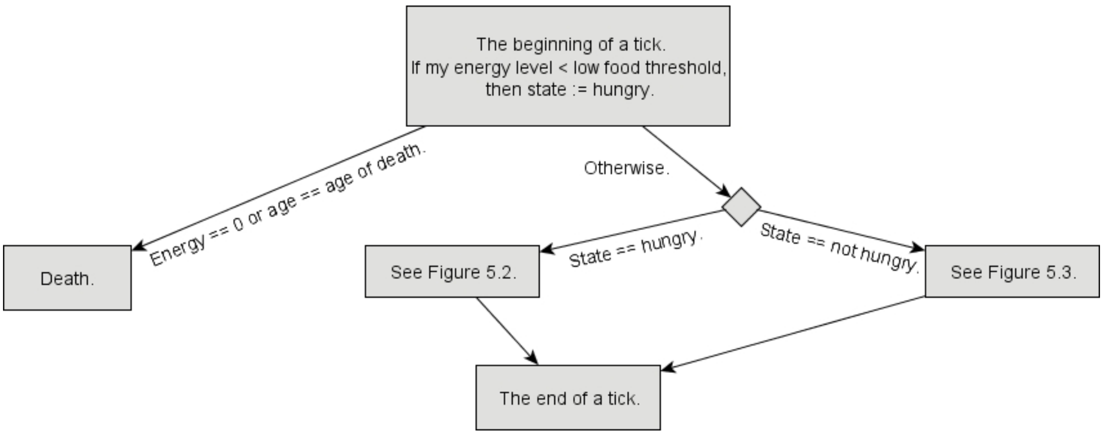

Figure 5.1: Cockroach action-selection rules in Model 5.0. Two states are special, they are basically pointers to other two diagrams. All actions described in Figure 5.2 and Figure 5.3 are taken inside these two special states, i.e., after a cockroach finishes his hunger-specific action (specified in Figure 5.2 or 5.3), he continues to "The end of a tick" state in this main diagram.

Cockroach eating

. The mechanism of eating is similar to the one in 4.2.7. There is a small difference though. The formula is:

$$F_e = min\{F_p, \frac{e_{max} - e_{cur}}{e_f}, m_e\}$$

where all symbols except m_e have the same meaning as in 4.2.7; m_e is the value of `maximum eating`. We thought this constant important as it is not plausible

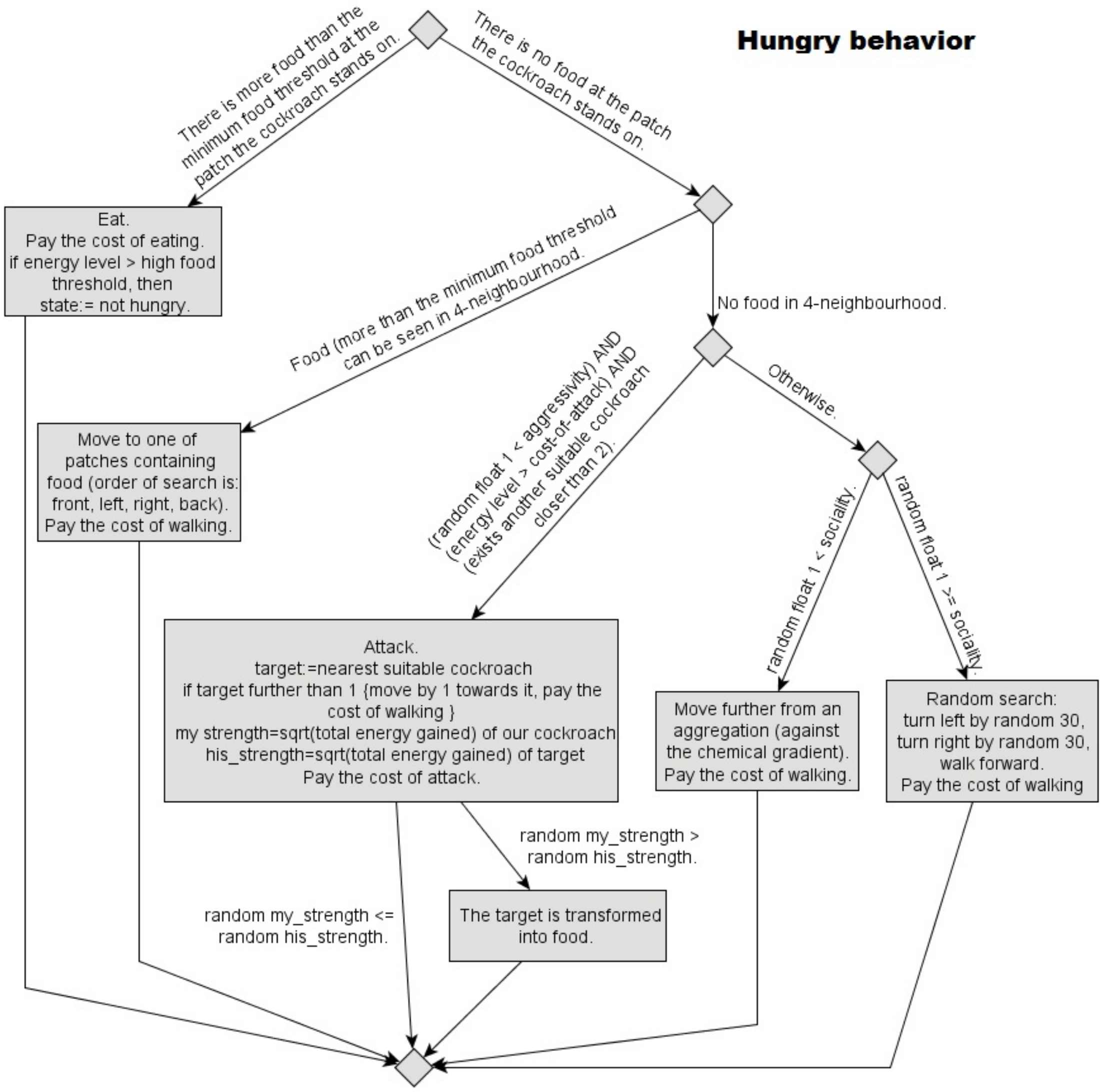

Figure 5.2: A part of cockroach behavior when a cockroach is hungry. This diagram is a part of Figure 5.1.

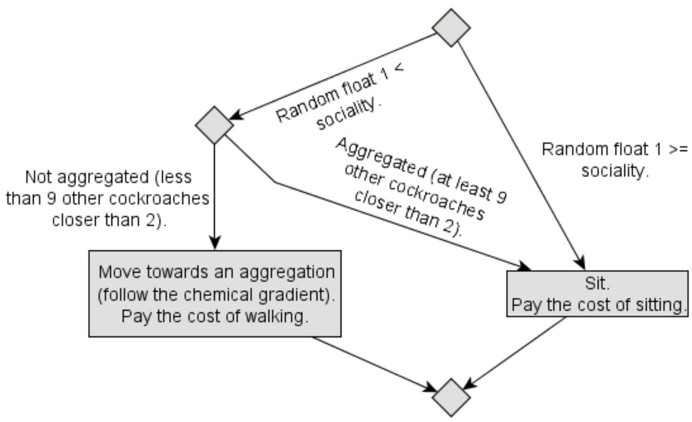

Figure 5.3: A part of cockroach behavior when a cockroach is not hungry. This diagram is a part of Figure 5.1.

that a single cockroach could devour whole another cockroach in a tick. When the quantity of food which may be eaten is limited in this way, corpses are more "shared" in an aggregation.

Cockroach fighting

In this model, cockroaches are capable of attacking and killing other cockroaches. First, a cockroach which succeeds in a test of aggressivity (i.e., random float 1 < `aggressivity` of the given cockroach) and has enough energy to attack has to find a suitable target. A suitable target is another cockroach closer than 2[10] with lower `total energy gained` than our cockroach's `total energy gained`. This represents the fact that modelled cockroaches attack only weaker cockroaches. When no such suitable target exists, our cockroach does not attack and looks in his 4-neighbourhood for food instead. If there is a suitable target, our cockroach will attack him (and if the target is further than 1, our cockroach moves towards him to attack). The fight is done in the following way: Both fighters measure their strength which is $\sqrt{\texttt{total energy gained}}$[11]. Then, both fighting cockroaches generate a random integer from the interval [0, strength). The one with higher number generated wins. If the attacker has won, the defender is transformed into food. If the attacker has lost, he is considered retreating and saves his life (he still pays the energy cost of attacking). This is based on thinking that the attacker attacks only weak cockroaches which are not too big threat (Daniel Frynta, personal communication, 18.5.2011). However, we will test even the possibility when an attacker may die.

Death

When a cockroach dies, he leaves his corpse in the environment, the corpse is a source of food for other cockroaches. See 4.3.1 to see how the corpse is transformed.

Reproduction

This phase represents the phase 5 of 5.2.3. All non-hungry (i.e. with `is hungry` = 0) cockroaches may reproduce. The probability that a non-hungry cockroach will reproduce is:

$$p_r = b_{rp} \cdot \frac{s}{10}$$

where p_r is the reproduction probability, b_{rp} is the `basic reproduction probability` and s is the *strength* of the cockroach trying to reproduce. It is a derived variable, value of which is equal to the square root of `energy eaten`. Such a formula for reproduction was created to reflect the fact that stronger cockroaches reproduce more easily.

[10]As in the previous chapter, let us note that whether "closer" means truly "closer", or "closer or equally distant" is not known as it is hidden inside the implementation of NetLogo. However, since we operate with float coordinates, the difference should be little to none.

[11] We thought that strength of cockroaches is not linearly proportional to the amount of food they have eaten, but that the growth is slower. However, the results were qualitatively similar when we tested logarithmic and linear dependence.

When the cockroach reproduces, new cockroach is created next to him. The parent splits his energy into two halves[12], keeps a half, the other half is gained by the child cockroach. The value of `sociality` is inherited and mutated, other variables of the child cockroach are set to values of the parent (among others, `aggressivity` of the parent is gained).

The mutation works in the following way:

$$s_c = s_p + random\ float\ 0.05 - random\ float\ 0.05$$

[13] where s_c is the value of `sociality` of the child cockroach and s_p is the value of `sociality` of the parent cockroach. If s_c should be lesser than 0, it is rounded to 1. Similarly, should it become larger than 1, it is rounded to 1.

Aging

This phase represents the phase 6 of 5.2.3. See 4.2.7 for its description. Note though, that we have changed the value of `maximum age` in this model. See 3.2.7 for its description.

Pheromone dispersion

This phase represents the phase 7 of 5.2.3.

5.3 Model variants

The previous section described the basic model of cockroach aggression, Model 5.0. This section describes extensions and modifications of this basic model. These extensions were created with the purpose of further understanding of the phenomenon of cockroach aggregation and for testing the hypotheses 5.1.3 and 5.1.2.

5.3.1 Model 5.1

In the model 5.0, food is added, more or less, all the time. How would cockroaches react to periods with no food added to the system? We call such a model of food addition *seasonal food*: there are *food seasons* and *starvation seasons* and these two are periodically rotated.

Environment changes

The food addition mechanism is changed. In food seasons, the mechanism of food addition is the same as in Model 5.0. In starvation seasons, no food is added at all (but corpses of cockroaches may still be created and eaten).

[12]This 50:50 ratio has been chosen arbitrarily, we do not know biologically plausible values.

[13]This leads to a slower mutation than in case of Model 2.1, we thought that jumps in Model 2.1 were perhaps too large.

State variable changes

Two environment parameters have been added: `starvation age length` and `food age length`. Those parameters determine the duration of the starvation season and food season.

Two environment variables have been added: `starvation counter` and `food season counter`. These represent, when in a given season, how much longer will the season last.

5.3.2 Model 5.2

This model serves as the platform for testing the invasibility of aggressive and nonaggressive cockroach populations, i.e., we will use it to test the hypothesis 5.1.2.

Environment changes

There are no changes in the environment.

State variable changes

The initialization of `sociality` and `aggressivity` is different from Model 5.0, as well as the method of their inheritance.

In the model 5.1, `aggressivity` of cockroaches has been always set to the value of the environment parameter `social aggressivity`. This is not true anymore in the model 5.2. Still, cockroaches are created in the initialization phase with their `aggressivity` equal to the value of `social aggressivity`. After the initialization, however, their `aggressivity` is inherited (without changing, no mutation occurs). This way, when a group of cockroaches with different `aggressivity` is added to the system, it may be observed which of the two values of `aggressivity` will evolutionarily prevail.

Furthermore, asocial cockroaches (with `sociality` 0) may be created in the system. It is important to know whether social cockroaches are invasible by asocial cockroaches or not.

The initial value of `sociality` was random in the previous models, which is not true in this model. Here, all social cockroaches start with `sociality` = 0.9. The value of `sociality` is, as in case of `aggressivity`, inherited and not mutated. This way, when a population of social cockroaches is put against a population of asocial cockroaches, it is easy to see which will prevail.

5.3.3 Model 5.3

The purpose of this model is to test the parallel evolution of `aggressivity` and `sociality` in cockroaches, i.e., to test the hypothesis 5.1.4.

Environment changes

There are no changes in the environment

State variable changes

The model is very similar to the model 5.0, except that `aggressivity` is evolved in a very similar way to the evolution of `sociality`. The value of `aggressivity` is inherited and mutated. The `aggressivity` of a child cockroach is:

$$a_{cc} = a_{pc} + random\ float\ 0.05 - random\ float\ 0.05$$

where a_{cc} is the value of `aggressivity` of the given child cockroach and a_{pc} is the value of `aggressivity` of his parent.

5.3.4 Model 5.3.1

In the model 5.3, when two cockroaches fight and the attacker loses, he only pays the price for attacking and he is not punished further (i.e., he withdraws[14]). It could be objected that certain species of real cockroaches behave differently and the attacker may be killed too (and his corpse is eaten). Furthermore, some animals may behave in this way when fighting (even the attacker may be killed), so if we want our results to be generalizable and not cockroach-specific, we consider it wise to understand such a model of fighting as well. Therefore, in this model, the attacking cockroach dies when he loses.

Environment changes

There are no changes in the environment.

State variable changes

There is a new environment parameter introduced: `cowardice`. In Model 5.3, when a cockroach determines his state for a given tick, he perceives if there are other, weaker cockroaches around. The value of `cowardice` determines, how much weaker a cockroach must be so that he is considered “weaker”. The dependence of weakness on `cowardice` is linear. E.g., with `cowardice` = 1, a cockroach is willing to attack any cockroach with lower strength than his. With `cowardice` = 2, the cockroach is willing to attack cockroaches with at most half his strength.

5.4 Description of experiments and their results

In this section, several experiments with various models are described. Initial values of state variables in the following experiments are, unless written otherwise, specified in Table 5.1 and Table 5.2.

After an experiment is described, it is followed by its results. The summary of all results is to be found in Discussion in this chapter. However, our results suffer from lack of statistical analysis of statistical significance of our results as we did not have enough time. Therefore, we often base our analysis on the observation of boxplots.

[14]This model of fighting is based on the observation of real cockroaches, where the attacker is very rarely killed (Daniel Frynta, personal communication, 18.5.2011).

5.4.1 Experiment 5.0: Testing aggressivity

Model 5.0 runs for 100 000 ticks (about 200 generations, the model is generally stable from 20-30000th tick; "generally" means that oscillations of `sociality` are noticeable, the size of the population oscillates only very slightly). After this time, the results are collected. They consist of (all measured in the last tick[15].):

- The value of `number of cockroaches` .
- The sum `energy level` of all living cockroaches.
- The mean `sociality` of cockroaches.
- The percentage of non-aggregated cockroaches. We define it as the number of cockroaches with less than 3 other cockroaches closer than 2. This percentage is measured, because we have observed that `sociality` is not an absolute measure of aggregation anymore (i.e., cockroaches with lower sociality were more aggregated).
- Moves of cockroaches: How many walking, sitting, eating and attacking moves have occurred in the last tick.

The input parameter is the value of `social aggressivity` which determines how aggressive will cockroaches be. We will test several values of this parameter: 0, 0.5, 0.1, 0.15, 0.2, 0.25, 0.3, 0.4. The simulation with every configuration of `social aggressivity` has been repeated 40 times for better statistical credibility.

5.4.2 The results of Experiment 5.0

The idea of this experiment was to show how various values of `social aggressivity` (i.e., overall aggressivity of the population) affect the behavior of cockroaches. Before we venture into the analysis of our results, we have to note that for values of `social aggressivity` 0.25, 0.3 and 0.4, very few or no cockroaches have survived whole 100 000 ticks (which is not the state in nature, if cockroaches were so aggressive they have extinguished themselves, they would not be in today's world at all). Therefore, these populations, although included in our graphs, are not too important in general.

Surviving cockroaches and total energy gained.

Looking at Figure 5.4, we see that certain values of `social aggressivity` have led to at least as good (for cockroaches) results as `social aggressivity` = 0, maybe even slightly better. Too high values of `social aggressivity` leads to less or no cockroaches surviving at all. Something of a breakpoint is the value 0.2 of `social aggressivity`. Here, the population was very large sometimes, while at other times, all cockroaches have died.

[15]It would be probably better to measure the data over time from a certain point of stabilization. We measured moves in the last tick only for reasons of available computational time. Nevertheless, since the experiment has been repeated 40 times, even the data about the last tick only are valuable and should be rather representative.

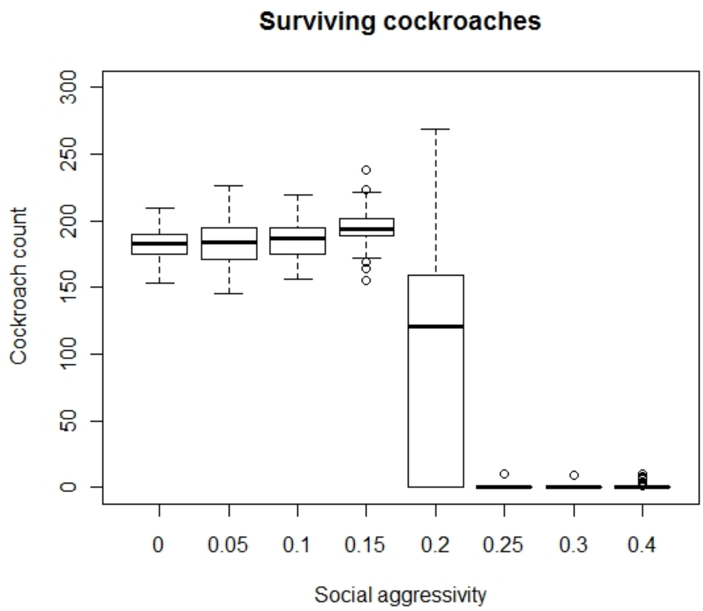

Figure 5.4: How many cockroaches have survived the experiment.

An explanation is: There is an advantage conferred by cockroach aggressivity (which will be described later), however, there is a disadvantage too: more energy is burned when cockroaches are aggressive and more cockroaches are killed overall (the latter is probably much more important).

When the value of `social aggressivity` is lower (i.e., $\leq$0.15), the advantage balances (or overweights) the disadvantage. When the value of `social aggressivity` is higher (i.e., ≥ 0.25), the opposite is true.

Let us note that the precise value of `social aggressivity` which is most advantageous to cockroaches, depends on their reproduction rate. If the cockroach reproduction has been slower than in our model, the ideal value of `social aggressivity` would be lower as the disadvantage caused by cockroaches dying would be more powerful. Similarly, if cockroaches reproduced faster, the ideal value of `social aggressivity` would be higher.

The overall number of cockroaches surviving is one measure of cockroach "fitness". Another measure is the sum of `energy level` of all cockroaches living at the end of the experiment. It could be thought to be something of "reproduction strength" as cockroaches containing more food tend to reproduce more. Another intuition is a "cockroach health".

The dependence of the sum of `energy level` on `social aggressivity` is depicted in Figure 5.5. We can see that the pattern is somewhat similar to the pattern in Figure 5.4, but more pronounced. It seems there is a trend that small positive values of `social aggressivity` benefit the cockroach population, while large values lead to too much killing (and little or no cockroaches surviving at all).

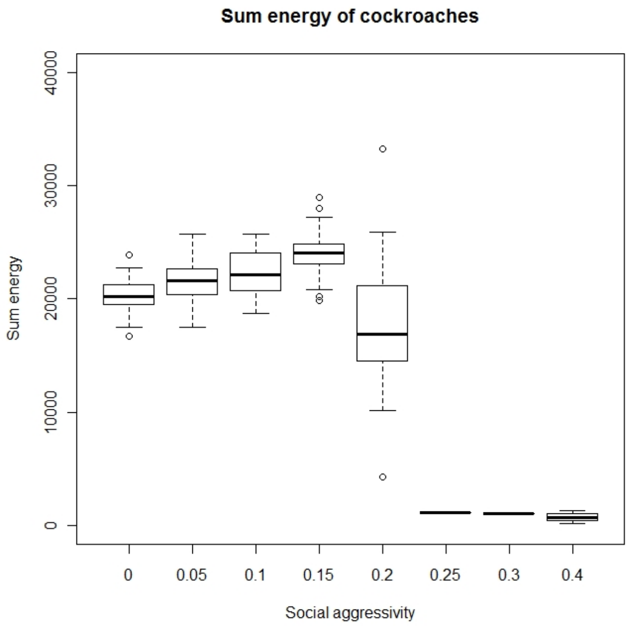

Figure 5.5: The sum of `energy level` of all living cockroaches at the end of the experiment.

Movement analysis

In this section, we will have a look at the dependence of cockroach movement (how much they walk, eat, etc.) on the value of `social aggressivity`. This dependence is depicted in Figure 5.6. We will not analyze too high values of `social aggressivity` as mostly all cockroaches died, so our data are very small and possibly unreliable. However, as we stated above, these values of `social aggressivity` are hardly plausible because if real cockroaches were so aggressive, they would be probably dead these days.

The most important result (and one of the most interesting results in this thesis) is, that reasonably aggressive cockroaches (e.g., `social aggressivity` $= 0.1$ or 0.15) walked less and sat more during their life[16] than nonaggressive (`social aggressivity` $= 0$) cockroaches do. This is very important as walking moves are more energetically expensive than sitting moves. We believe that this is the advantage of aggressivity and it is why reasonably aggressive populations were more slightly more successful (marginally more numerous and containing more food) than nonaggressive populations. When aggressive cockroaches find food, they use it more effectively than nonaggressive cockroaches (they live longer from it).

There is very little difference in eating percentage of cockroaches with `social aggressivity` ≤ 0.25, with nonaggressive cockroaches maybe eating a bit more often. There is a possible explanation that aggressive cockroaches eat corpses of other cockroaches more than nonaggressive cockroaches do. A corpse is often

[16] We have measured the number of moves in the last tick only. However if we presume that the system is rather stable at the time when it has been measured and that we repeated the experiment 40 times, we may generalize this result to other ticks than the last tick of the experiment only.

very large amount of food, therefore when a corpse is eaten, a lot of food is eaten, therefore it will last longer before the cockroach has to eat again.

On the other hand, aggressive cockroaches attack more than nonaggressive ones (obviously), but the overall percentage of attacks is very small.

Nevertheless, we consider the percentage of sitting and walking more important than the percentage of eating and attacking. But why do aggressive cockroaches sit more (and walk less) than the nonaggressive cockroaches? We believe that as the concentration of cockroaches is high in an aggregation, cockroaches are mostly killed in an aggregation too, or in its close vicinity. Therefore, many cockroaches may find the food from cockroach corpses easily and they do not have to walk to far to get it.

Back in results of Experiment 2.1, i.e., in section 4.5.2, we said that aggregation is advantageous as corpses are shared more effectively. The mechanism of reasonable cockroach aggressivity basically makes the concept of corpse sharing even more effective (even more corpses are present near an aggregation). Of course, more cockroaches die when the population is reasonably aggressive, but as the aggregation as a whole is more effective and does not spend so much energy on walking, it may put the spared energy into the creation of new cockroaches. We have shown that this positive influence of more cockroaches being created may prevail over the disadvantage of more cockroaches being killed, when the aggressivity is not too high (in such a case, the disadvantage prevails).

Our results support the part of Hypothesis 5.1.1 concerning energy efficiency. Further statistical analysis would be necessary to decide whether the growth of population size in Figure 5.4 is statistically significant.

Sociality and aggregation.

While the fact that reasonable cockroach aggressivity could lead to larger cockroach population is interesting, it is necessary to know, whether aggressive cockroaches still aggregate: Real cockroaches are social as well as slightly aggressive, if we have created a successful population of asocials, it would not be plausible.

It could be a surprise that, looking at Figure 5.7, it seems that values of `social aggressivity` of 0.05–0.15 leads to lower `sociality` of cockroaches (still very high though) than with `social aggressivity` = 0. We wondered why this happens, particularly because we visually observed aggressive cockroaches (in the model, not in nature) and they seemed to aggregate more than asocial cockroaches. That is why we measured the percentage of non-aggregated cockroaches in the population too, it is depicted in Figure 5.8. Therefore, reasonable aggressivity leads to cockroaches behaving more aggregatively, even though their `sociality` is lower[17].

[17] We believe that an explanation of this phenomenon is that cockroaches with lower sociality "aggregate" with other cockroaches indirectly (not because they would prefer aggregations, but because there is food). There are many dead cockroaches in aggregations and nearby, therefore when less social cockroaches "wander" into an aggregation, they may eat there and sit there for a long time, waiting.

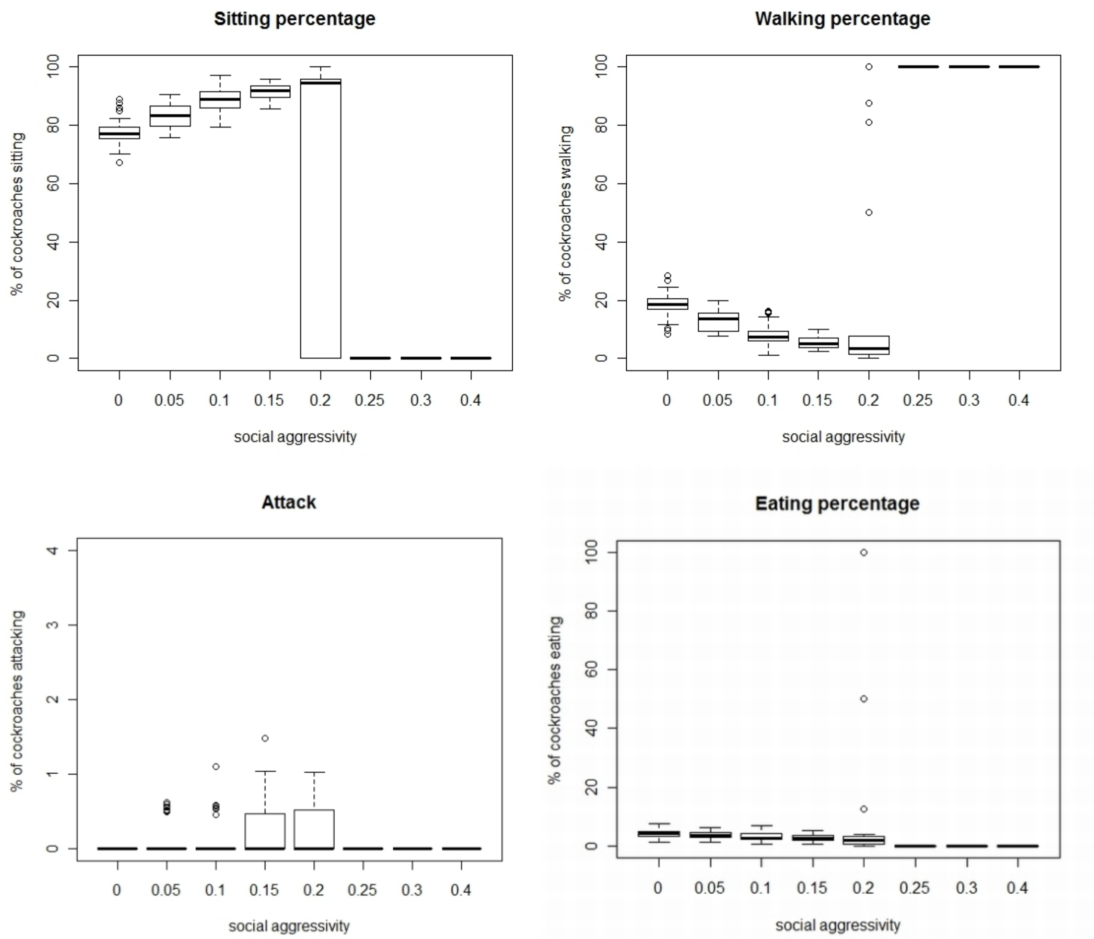

Figure 5.6: How many of various moves (walking, sitting, eating, attacking) have cockroaches made in the last tick of Experiment 5.0. The results are in percents. Note that the y-scale of Attack graph is different from other graphs.

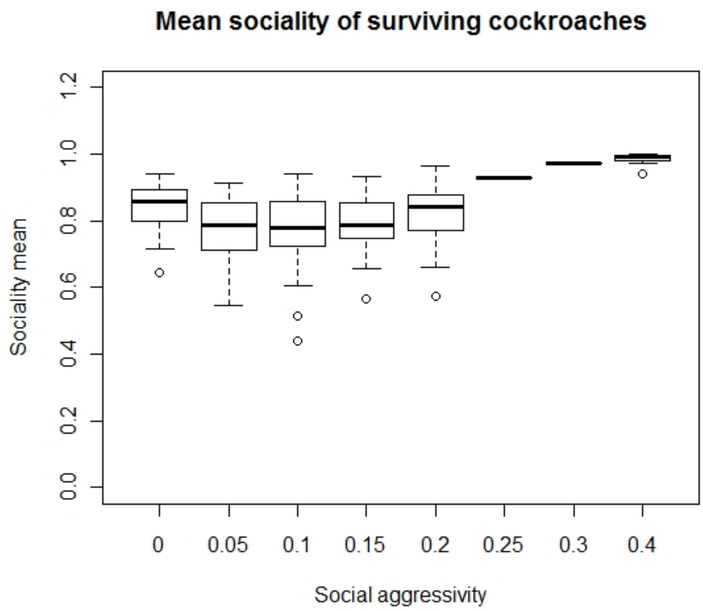

Figure 5.7: Mean `sociality` of cockroaches at the end of Experiment 5.0 is depicted in this figure.

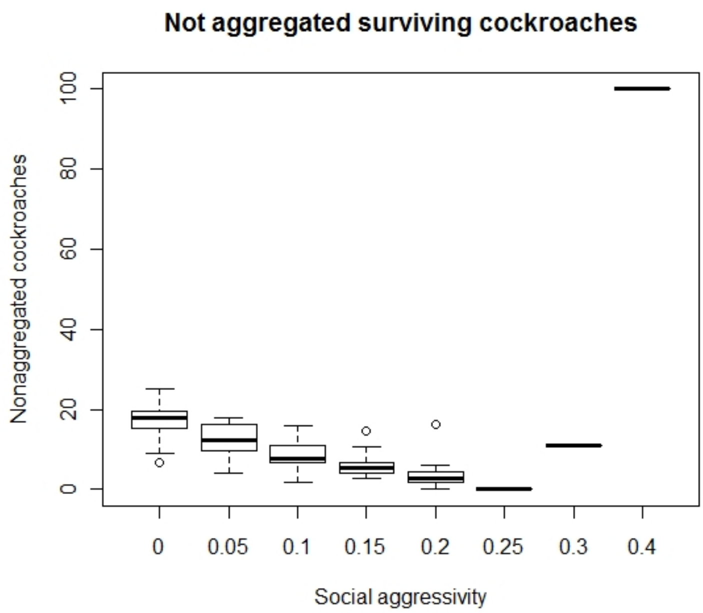

Figure 5.8: How many cockroaches in the environment were not aggregated (measured in percents) in the last tick of Experiment 5.0. “Not aggregated cockroach” is a cockroach with less than three cockroaches closer than 2 space units.

5.4.3 Experiment 5.1: Testing seasonal food

In this experiment, a population of cockroaches from Model 5.1 tries to survive periods when no food is added to the system. There are two populations tested: the first is a population of nonaggressive cockroaches, having `aggressivity` 0. The other population is a population of slightly aggressive cockroaches, having `aggressivity` 0.1. Both populations will be put through a set of tests.

There are six different *subexperiments*: six different setups of `food age length` and `starvation age length`. However, it is not possible to throw a cockroach population into an era of long starvation immediately as the population would die right away (even though it is perfectly capable of surviving it after it stabilizes). For this reason, we start the experiment with `starvation age length` = 0 and let the cockroach population stabilize for 15 000 ticks. Then, we change the values of `starvation length` and `food age length` according to Table 5.3.

The value of 15 000 ticks is not the only one when `starvation length` and `food age length` are changed. In certain subexperiments, both ages are made very long, i.e., values of `starvation length` and `food age length` are high. Why not to set these `starvation length` and `food age length` to these values in the tick 15 000 already? The reason is that such a sudden change (no starvation → very long starvation) would often kill the cockroach population while if we raise values of `starvation length` and `food age length` gradually to high values, cockroaches often survive it. We do not want our cockroaches to die because we changed the length of `starvation age length` too steeply. If they die, they should die in time and prove they are not capable of surviving in such conditions. Therefore, in latter subexperiments, we raise the length of both ages gradually.

Subexperiment	Changes made in the following moments of the experiment			
	15000	30000	45000	60000
1	100	-	-	-
2	500	-	-	-
3	500	1000	-	-
4	500	1000	1300	-
5	500	1000	1500	-
6	500	1000	1500	2000

Table 5.3: Here, there are written the changes of `food age length` and `starvation age` in various moments (ticks) of the run of the experiment (for simplicity, both parameters are set to the same value). The symbol "-" means that no change is made in the given tick.

Both tested populations, aggressive and nonaggressive, will run through all six subexperiment. The length of each subexperiment is 200 000 ticks (which is quite a long time). After a subexperiment ends, it is measured whether any cockroaches have survived it. When all data are collected, we will compare how many aggressive cockroaches survived the given subexperiments compared to nonaggressive ones.

A run of a given population in a given subexperiment has been repeated 40 times for better statistical credibility (i.e., 6 parameter setups, 2 different populations and 40 repeats of each yields 480 runs in total).

5.4.4 The results of Experiment 5.1

In Experiment 5.1, we wanted to determine whether aggressive cockroaches are better at surviving periods of time with no food added to the environment. Several different lengths of such periods were tested, see 5.4.3 for their definition. The results of all such subexperiments are in Table 5.4.

Subexperiment number	% of surviving nonaggressive cockroach populations	% of surviving aggressive cockroach populations
1	100	100
2	100	100
3	100	92.5
4	55	45
5	32.5	67.5
6	7.5	55

Table 5.4: This table contains the percentage of aggressive and nonaggressive cockroach populations surviving a given subexperiment.

In subexperiments 1 and 2 where the values of `starvation age length` and `food age length` are the smallest, there is no difference between aggressive and nonaggressive cockroaches as all populations survived.

In subexperiments 3 and 4, nonaggressive populations were slightly more successful (i.e., they have survived more often) than aggressive ones. The reason for this is, it seems, that aggressive cockroaches with fixed aggressivity have slightly more trouble surviving sudden changes of `starvation age length`. When a population of aggressive cockroaches died, it was right after such a change[18] – cockroaches ate one another too much. It seems that this problem is mostly caused by the fact that `aggressivity` of cockroaches was fixed. When we ran similar experiment with model where `aggressivity` was evolved, cockroaches have spontaneously lowered their aggressivity in times when it would be disadvantageous to be aggressive. This led to aggressive cockroaches surviving sudden changes of `starvation age length` more easily.

In subexperiments 5 and 6, where the value of `starvation age length` was highest, the populations of aggressive cockroaches survived much more than the populations of nonaggressive cockroaches. It seems indeed, as we predicted, that in times of crisis, nonaggressive cockroaches were running around the environment, searching for food which was not there, burning excessive amounts of energy. On the other hand, aggressive cockroaches were running much less[19] as a lot of food was present in their aggregations. Therefore, Hypothesis 5.1.3 has been supported by our data.

[18] We believe that this could be an explanation: When there is a change of `starvation age length`, aggressive cockroaches start attacking one another to get food. After a while of killing, there is enough corpses (critical amount) in aggregations and aggressive cockroaches mostly sit and live effectively. However, sometimes they extinguish themselves when creating the critical amount of corpses.

[19] These results are based on visual observation of the model.

5.4.5 Experiment 5.2: Testing invasibility

In this experiment, a population of cockroaches from Model 5.2 lives for 15 000 (which is enough to stabilize itself). Then, a competing small population (20 cockroaches) of different cockroaches is inserted into the environment. The experiment ends when the time of 50000 ticks[20] is reached, or one populations is extinguished. At the end of the experiment, average values of `sociality` and `aggressivity` are collected; from them, it may be deduced which population has won. E.g.: If the former population had `sociality` = 0 and the invading population had `sociality` = 1, if, at the end of the experiment, is the average `sociality` = 1, we know that the invading population has won.

The competing population is created in such a way that `age` of invading cockroaches is equal to random 1000 and their `energy level`, as well as their `total energy gained` is equal to `maximum energy level`. These values have been chosen so that the invading population consists of similarly strong cockroaches as the former population does.

Which populations (how parametrized) will be tested against which is described in Table 5.5. We designed these populations to test wide range of populations having different `aggressivity` and `sociality`. Every competition between two populations is called a *subexperiment*. The computation of each subexperiment has been repeated 40 times for better statistical credibility.

Subexperiment number	f.p. `sociality`	f.p. `aggressivity`	c.p. `sociality`	c.p. `aggressivity`
1	0.9	0	0	0
2	0.9	0	0	0.1
3	0.9	0	0.9	0.1
4	0.9	0.1	0	0
5	0.9	0.1	0	0.1
6	0.9	0.1	0.9	0
7	0.9	0.1	0.9	0.3

Table 5.5: This table describes various configurations of the two populations competing in Experiment 5.2. The abbreviation "f.p" means former population (starting in the environment), "c.p" means competing population (the population inserted into the environment later).

5.4.6 The results of Experiment 5.2

The results of all subexperiments are in Table 5.6.

The first subexperiment yielded results which were only to be expected[21]. It shows that a population of social nonaggressive cockroaches is immune to an invasion of asocial nonaggressive cockroaches. In other words, it shows that a social strategy is not invasible by an asocial strategy.

[20] Preliminary research has shown that this value should be high enough and that it will be easy to recognize the winning population.

[21] Since there is no aggressivity in the subexperiment, it is a competition of social and asocial cockroaches, similar to Model 2.1. In Model 2.1, high `sociality` has been evolved, therefore we believe that high sociality would be more advantageous to cockroaches.

Subexperiment number	Wins	Losses	Ties
1	40	0	0
2	40	0	0
3	1	9	30
4	40	0	0
5	40	0	0
6	39	0	1
7	35	0	5

Table 5.6: This is a table of results of single competitions between various populations. Wins, losses and ties relate to the former population, e.g., if the former population "has lost", it means it has been extinguished by the invading population. A tie means that cockroaches of both populations were present in the environment at the end of the subexperiment.

The second subexperiment was more interesting: social nonaggressive cockroaches were invaded by a population of asocial aggressive cockroaches. The social cockroaches have won all the competitions in this experiment. Therefore, slight aggressivity still does not outweigh the disadvantage of asocial behavior over social behavior.

In the third subexperiment, social aggressive cockroaches have invaded social nonaggressive cockroaches. The invasion was mostly successful as the former population won only once and has been defeated nine times. It could seem that 30 ties indicate a semi-stable state of the environment, but most of these ties were almost-defeats of the former population[22]. If the subexperiment ran for a longer time, many of the given ties would become losses.

In the fourth subexperiment, a former population of social aggressive cockroaches faced an invasion of asocial nonaggressive cockroaches. Since it seems that being social is more advantageous than being asocial and being reasonably aggressive is more advantageous than being nonaggressive, it was expected the former population would dominate and this subexperiment supports this expectation..

In the fifth subexperiment, social aggressive cockroaches were invaded by asocial aggressive cockroaches. Every repetition, the former population has won. This suggests that when two populations are similarly aggressive, the sociality is still an advantage.

In the sixth subexperiment, we wanted to make sure that social aggressive population is not invasible by social nonaggressive population. If it was, it would be a very strange outcome indeed as it would mean that although cockroach aggressivity seems to be slightly beneficial, it would be invasible. However, the invasion of social nonaggressive cockroaches was almost always unsuccessful, the one exception, a tie, would probably end up as a loss too.

In the seventh subexperiment, we wondered whether a population of social aggressive cockroaches is not invasible by a population of social and very highly aggressive cockroaches, even though `aggressivity` $= 0.1$ seems much more advantageous than `aggressivity` $= 0.3$ evolutionarily. However, we thought it

[22] As our time for computations was limited, we ran all subexperiments for 50 000 ticks only. This subexperiment could be repeated when limited to 100 000 ticks, results would be probably clearer.

could happen that very aggressive invaders would extinguish the former population and then live ineffectively (or wipe themselves out). Nevertheless, the former population of less aggressive cockroaches has almost always destroyed the invading population. In the case of five ties, it would be probably only a matter of time before the less aggressive population would prevail. Therefore, reasonably aggressive cockroaches are not invasible by a population of fierce killers[23].

To conclude these results, even though social nonaggressive population seems reasonably resistant to invasions (or, at least, some of them), aggressivity makes it much more robust. Therefore, we believe that our data support Hypothesis 5.1.2.

[23] We believe that too aggressive cockroaches attack so often they are energetically inefficient, i.e., spend too much energy on attacking, compared to reasonable aggressive cockroaches.

5.4.7 Experiment 5.3: Testing evolution

In this experiment, a population of cockroaches from Model 5.3 is created and lives for 100 000 ticks. After this time, the results are collected. They consist of (all measured in the last tick[24]):

- The number of living cockroaches.
- The sum energy in all living cockroaches.
- The mean `sociality` of cockroaches.
- The mean `aggressivity` of cockroaches.
- The percentage of non-aggregated cockroaches. We define it as the number of cockroaches with less than 3 other cockroaches closer than 2. This percentage is measured, because we have observed that `sociality` is not an absolute measure of aggregation anymore (i.e., cockroaches with lower sociality were more aggregated).
- Moves of cockroaches: How many walking, sitting, eating and attacking moves have occurred in the last tick.

The experiment has been repeated 40 times as the experiments before.

5.4.8 The results of Experiment 5.3

Similar things have been measured as in Experiment 5.0.

The purpose of this experiment was, among others, to test, whether the results of Experiment 5.0 were not caused by the fact that `aggressivity` of cockroaches was fixed (it was always equal to `social aggressivity`). I.e., we wondered whether when we let cockroaches evolve their `aggressivity`, will they self-regulate their aggressivity, so they do not become 100% killers? Such a population would destroy itself quickly, which is not a very plausible behavior indeed.

Evolved aggressivity, surviving cockroaches and their total energy level

An example of how the evolution may look is in Figure 5.9The mean `aggressivity` evolved in cockroaches during the experiment is shown in Figure 5.10. The value is about 0.11, which is lower than 0.15 which seemed the most advantageous in Experiment 5.0. That is interesting and we are not sure about the right answer. We could be in some sort of local minimum

The evolved population seems to be slightly more successful than a nonaggressive population from Model 5.0 (tested in Experiment 5.0), see Figure 5.11 and Figure 5.12. Also, the fact that this evolving population survived at all is a very important result: It shows that a population of evolving aggressive cockroaches is capable of a sort of self-regulation; the evolved populations was not so aggressive to destroy itself. Slight aggressivity even seems to be slightly advantageous to cockroaches. At the first sight, it is counterintuitive that killing of other

[24]Again, as in Model 5.0, it would be probably measure these data as a "discrete integral" over time since stabilization of the model but we did not have enough time.

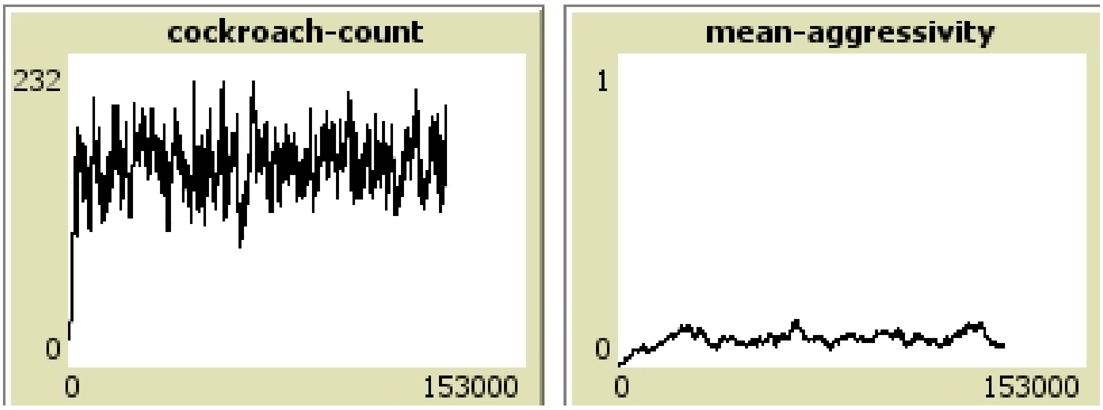

Figure 5.9: An example of evolution of total number of cockroaches and their mean `aggressivity` in Model 5.3.

cockroaches should lead to more cockroaches living in the population but we believe that the reasons stated in 5.4.2 are a good explanation of this interesting phenomenon.

Movement analysis

The pattern in Figure 5.13 is similar as the pattern of slightly aggressive cockroaches in Experiment 5.0, see 5.4.2. The important thing is that our evolved, slightly aggressive cockroaches still sit more and walk less than nonaggressive cockroaches.

Sociality and aggregation

Cockroach `sociality` evolved very similarly as in Experiment 5.0, see Figure 5.14. The same may be said for the number of nonaggregated cockroaches, see Figure 5.15. The resulting `sociality` is rather high and vast majority of cockroaches is aggregated. This fact yields an important consequence: cockroach aggressivity actually promotes aggregation.

It is interesting to see that even though cockroaches, as individuals, risk being in an aggregation where they may be killed, they still tend to aggregate as they evolutionarily "understand" it is advantageous to them. Their behavior is very altruistic in a sense: they bring food to their aggregation in their bodies, knowing that they will either help themselves (eat a corpse of another cockroach when they become hungry later), or help others (when being eaten after being killed by another cockroach or dying of age).

When experimenting with Model 5.3, we have made an interesting observation concerning the correspondence of cockroach `sociality` and `aggressivity`: The cockroaches with above-average `sociality` were noticeably more aggressive than the cockroaches with below-average `sociality` (the `aggressivity` of highly social cockroaches was about 3-4 higher than `aggressivity` of less social cockroaches). This leads to an emergent segregation of two kinds of cockroaches living in an aggregation: The first kind consists of aggressive cockroaches: these cockroaches mostly sit in the aggregation, kill incoming cockroaches and feed on their corpses. Then there is the second kind of cockroaches: not very aggressive,

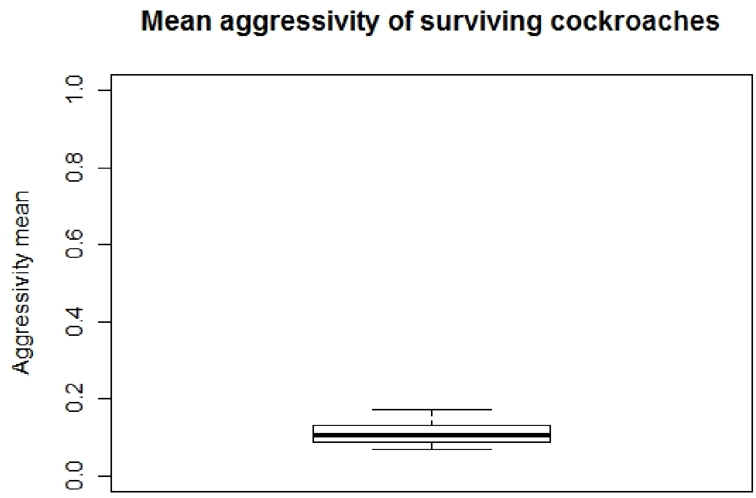

Figure 5.10: The evolved value of `aggressivity` among cockroaches in Experiment 5.3.

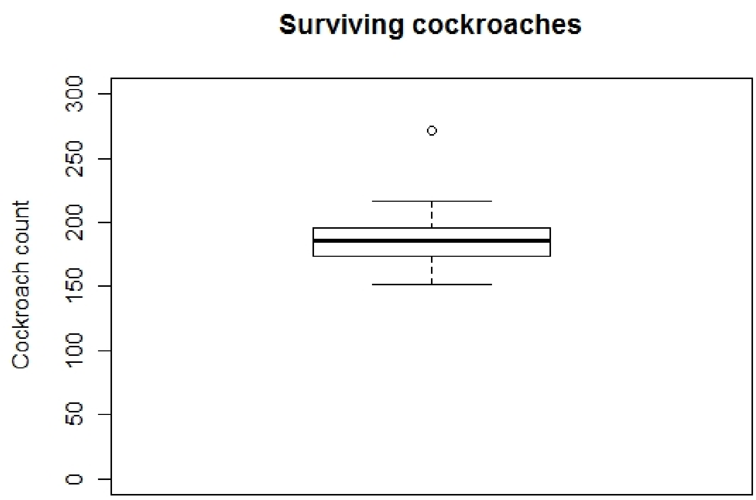

Figure 5.11: How many cockroaches have survived Experiment 5.3.

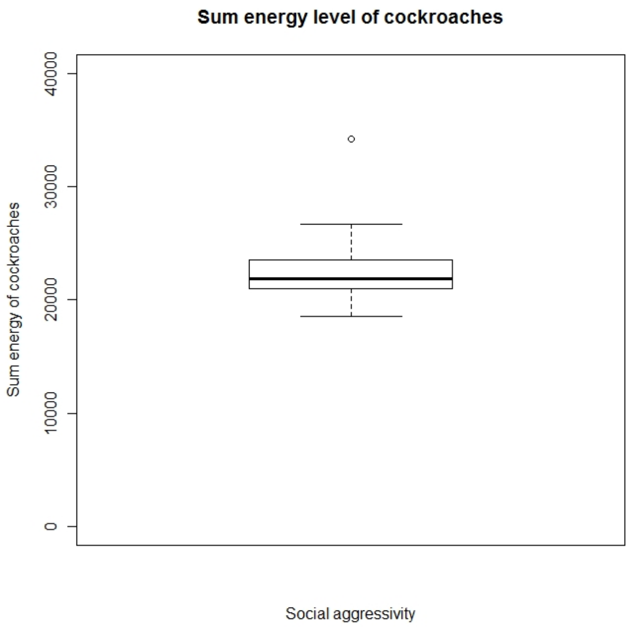

Figure 5.12: The sum of `energy level` of all living cockroaches at the end of Experiment 5.3.

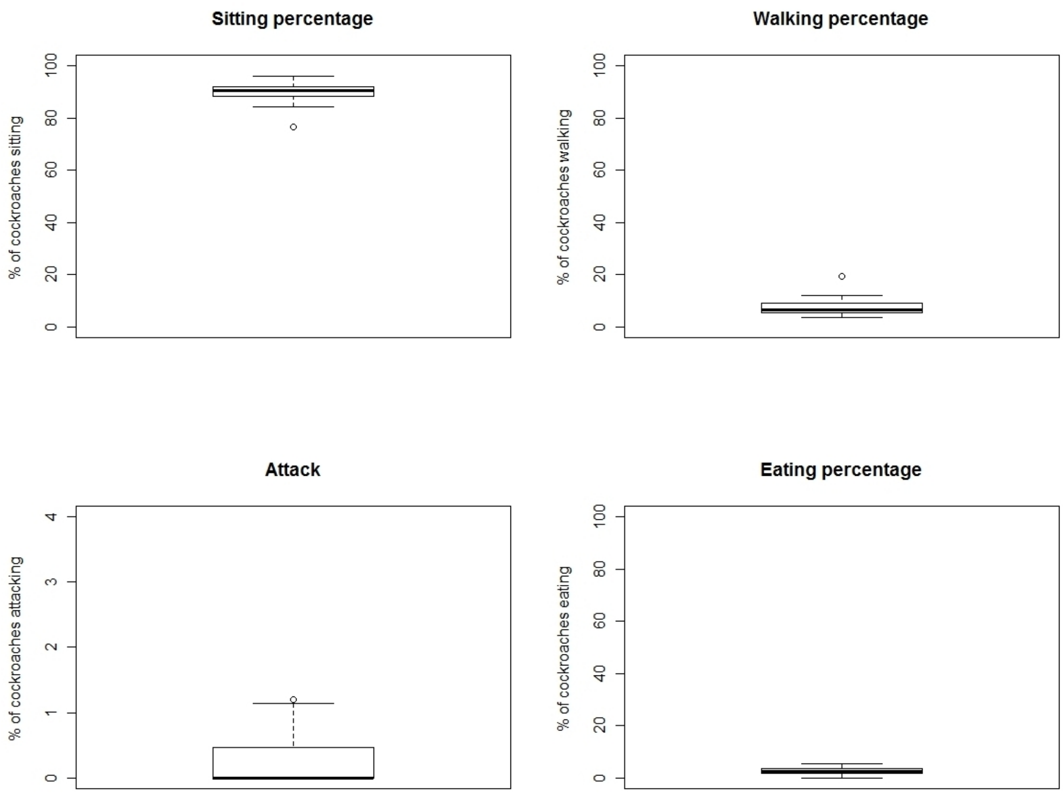

Figure 5.13: How many of various moves (walking, sitting, eating, attacking) have cockroaches made in the last tick of Experiment 5.3. The results are in percents. Note that the y-scale of Attack graph is different from other graphs.

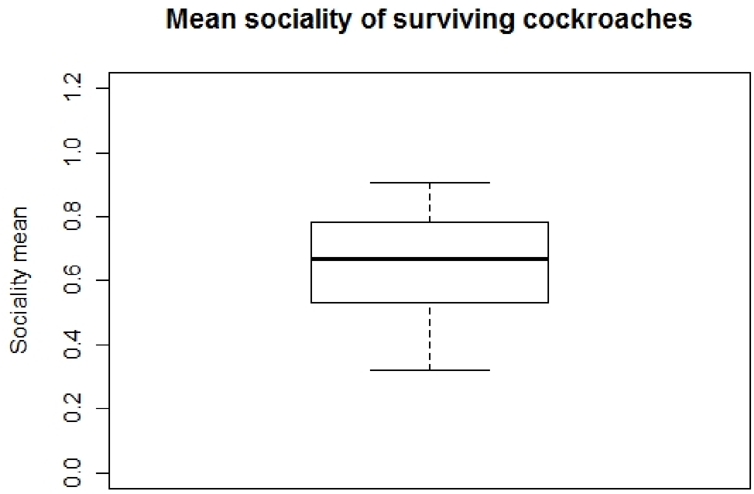

Figure 5.14: Mean `sociality` of cockroaches at the end of Experiment 5.3 is depicted in this figure.

more explorative kind of cockroaches. These cockroaches feed more on the food outside the aggregation. Then, they bring the food from outside to the aggregation inside their bodies. When killed by aggregated aggressive cockroaches, they actually bring the food collected into the aggregation.

Of course, this observation is an observation of our model only. It could be very interesting to observe whether there is similar social structure among real cockroaches.

The fact that cockroaches evolving their `aggressivity` and `sociality` at once formed aggregations is very important as it supports Hypothesis 5.1.4.

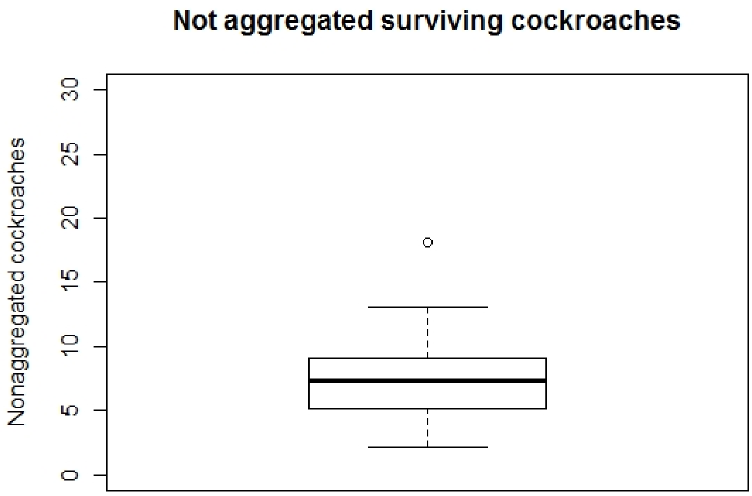

Figure 5.15: How many cockroaches in the environment were not aggregated in the last tick of Experiment 5.3 (measured in percents). “Not aggregated cockroach” is a cockroach with less than three cockroaches closer than 2 space units.

5.4.9 Experiment 5.3.1: Testing different fighting mechanism

This experiment is very similar to Experiment 5.3. It uses Model 5.3.1 instead of 5.3 and has one input parameter more: `cowardice`. There are five *subexperiments*, each with a different value of `cowardice`. Values of the `cowardice` parameter were: 0.1, 0.5, 1, 1.5, 2. Within each subexperiment, the cockroaches of Model 5.3.1 lived for 100 000 ticks. From each of these *subexperiments*, we have collected the same data as from Experiment 5.3.

The experiment has been repeated 40 times as the experiments before.

5.4.10 The results of Experiment 5.3.1

The experiment was, as suggested by its number, very similar to Experiment 5.3.1 (the same kind of data has been measured). However, the fighting model is different and we tested the dependence of measured data on several values of `cowardice`.

Surviving cockroaches, their total energy level and evolved aggressivity

Looking at Figure 5.16 and Figure 5.17 and comparing it with Figure 5.4 and Figure 5.5 we see that even the model of fighting where an attacker may die still suggests that aggressivity is at least as good as nonaggressivity, maybe even slightly advantageous (except `cowardice` = 2 where the difference is negligible, if any). However, the aggressivity in Model 5.3 seems to bring a larger advantage to cockroaches than the model of fighting from Model 5.3.1.

The results suggest that the value of `cowardice` 1.5 is the most advantageous from the measured values, but the difference from other values is very small indeed. Further statistical analysis would be necessary to decide upon its significance. Is it true that it does not matter how cowardly cockroaches behave? Absolutely not, the answer lies in Figure 5.18. Even though different values of `cowardice` lead to similar results in Figure 5.16 and Figure 5.17, this is because of different values of `aggressivity` which have evolved.

Before we wrote this thesis, we tested a variant of model 5.3.1 where the cockroach aggressivity did not evolve and was fixed. Surprisingly, aggressive cockroaches with low values of `cowardice` were the most successful. We have shown that it was because they created the most corpses in the aggregation (mostly corpses of attackers). The problem of the population (with `cowardice` = 0.1 and `aggressivity` = 0.5) was, that it was easily invasible. For example, social nonaggressive cockroaches have invaded them easily (even though they are less effective population). Why? A nonaggressive cockroach has a certain probability in his life that he will be killed by an aggressive cockroach. An aggressive cockroach may be killed by another aggressive cockroach too, but furthermore he has a probability he will die attacking (and the probability is very high with low values of `cowardice`). Therefore, aggressive cockroaches will die more. When their `cowardice` is high, they do not die as much and the advantage of aggressivity outweighs the disadvantage (higher death ratio). On the other hand, when their `cowardice` is low, they may be easily invaded by a population with lower death ration.

A population of aggressive cockroaches with low `cowardice` is a good example of why it is important to test invasibility and/or evolutionary model. Also, it is a good example of a population which works very well on its own, but when invaded by another (possibly inferior) population, it is easily beaten and destroyed.

Experiment 5.3.1 shows that evolution reacts to different values of `cowardice` by evolving different values of `aggressivity`. It is only to be expected, after all: the issue with aggressive cockroaches with low `cowardice` is they attack too much. When `cowardice` is fixed, `aggressivity` has to be changed so they attack less. Similarly, cockroaches with high `cowardice` lose very seldom in a fight, therefore their `aggressivity` may be higher.

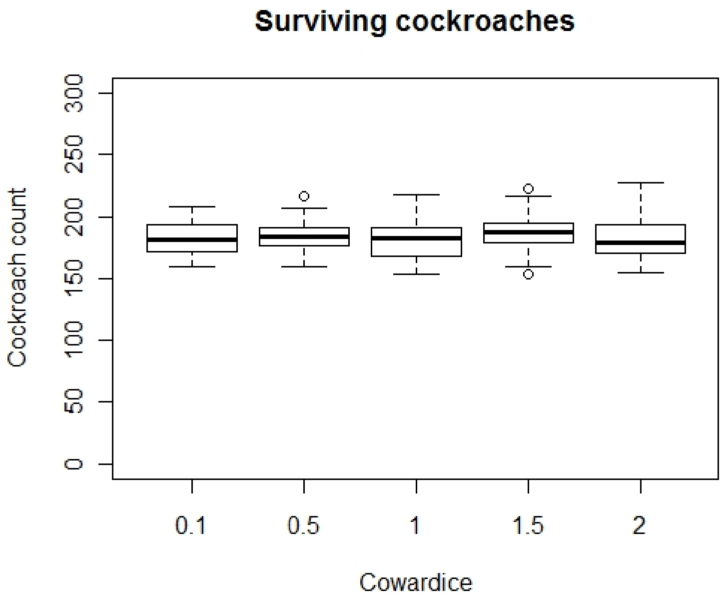

Figure 5.16: How many cockroaches have survived Experiment 5.3.1

Movement analysis

As in the case of surviving cockroaches and the sum `energy level` of cockroaches, the number of various moves is almost independent on the cockroach `cowardice` (but again, it is caused by the evolution compensating high `cowardice` by setting `aggressivity` lower and *vice versa*.). The value 2.0 is the only noticeably different value, a population having it sat less and walked more. Let us note that such a population was the least successful in means of surviving cockroach count and the sum `energy level`. It further bolsters our hypothesis that the success of a population is largely determined by its energy efficiency: how much do cockroaches walk and sit[25].

When compared to nonaggressive cockroaches (from Model 5.0), aggressive cockroaches from Model 5.3.1 sit more and walk less, which is probably why they are slightly more successful.

[25]These two moves relate to our model only. The idea of energy efficiency being so important may be generalized to other insects too. In other words, it may be interesting to try to explain behavioral rules of insects from the point of view of energy efficiency.

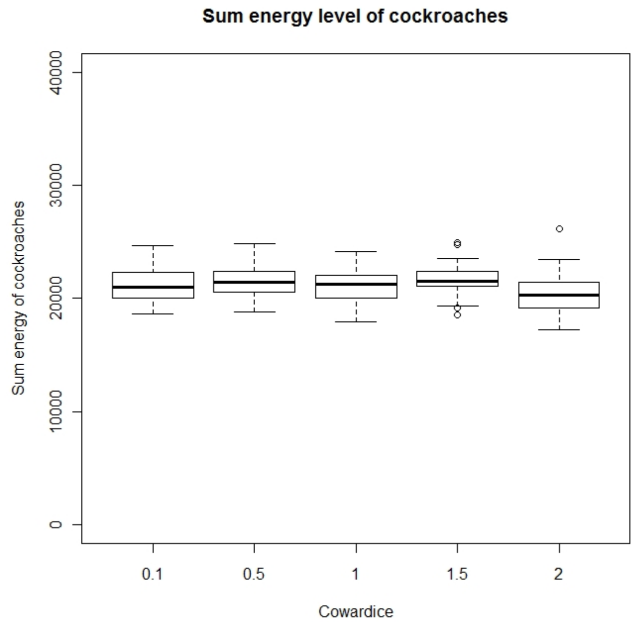

Figure 5.17: The sum of `energy level` of all living cockroaches at the end of Experiment 5.3.1.

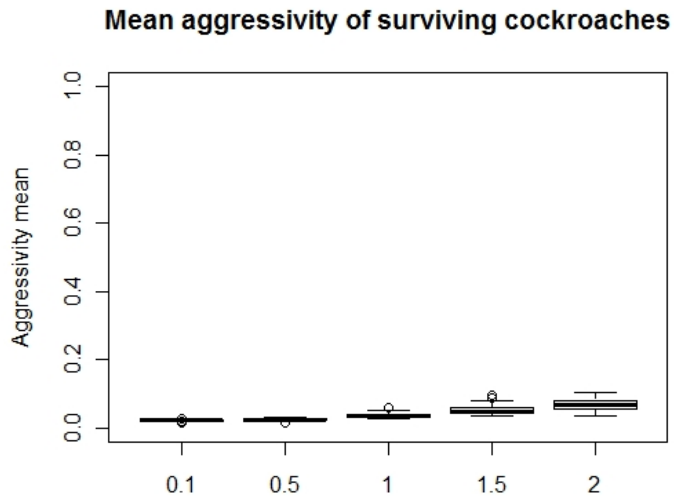

Figure 5.18: The evolved value of `aggressivity` among cockroaches in Experiment 5.3.1.

Sociality and aggregation

The model of fighting from model 5.3.1 leads, similarly to Model 5.3, to lower sociality and higher percentage of aggregated cockroaches than in the case of nonaggressive cockroaches from 5.0. Therefore, the result from Experiment 5.3, that aggressivity leads to more aggregative behavior holds true even in Model 5.3.1. However, the fighting mechanism of Model 5.3 led to even more cockroaches aggregating than the mechanism of Model 5.3.1.

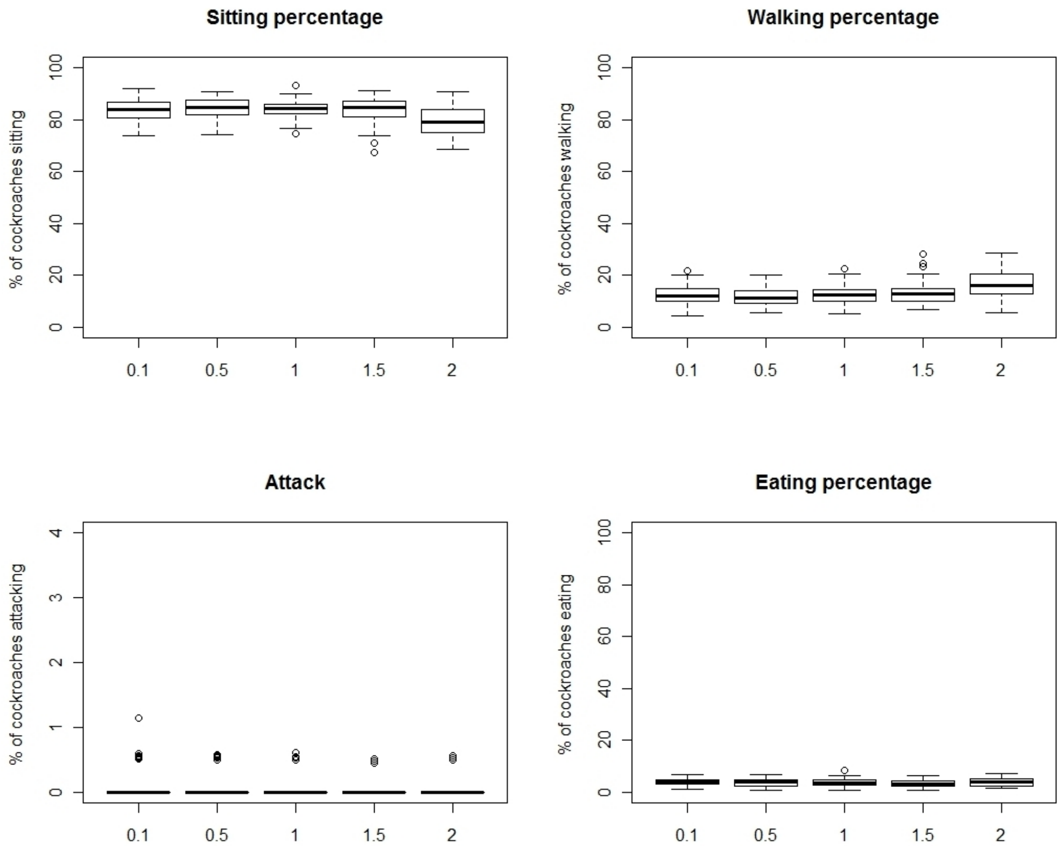

Figure 5.19: The numbers of various moves (walking, sitting, eating, attacking) that cockroaches have made in the last tick in Model 5.3.1. The results are in percents. Note that the y-scale of Attack graph is different from other graphs.

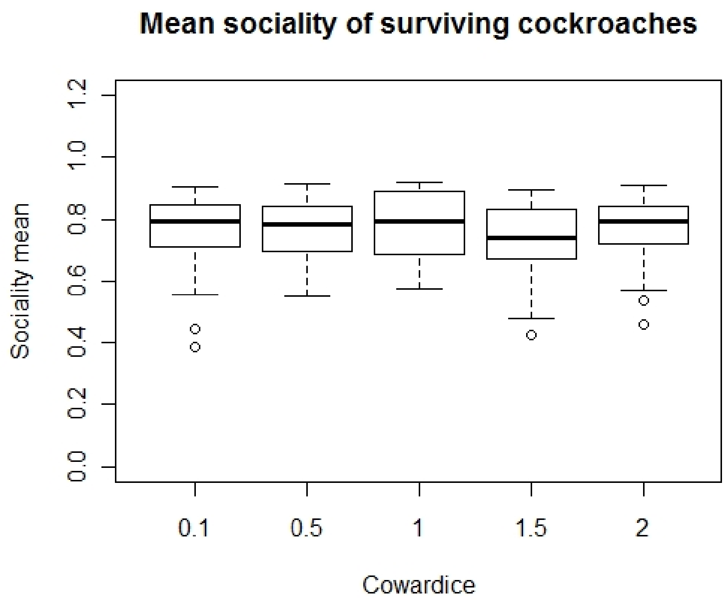

Figure 5.20: Mean `sociality` of cockroaches at the end of Experiment 5.3.1 is depicted in this figure.

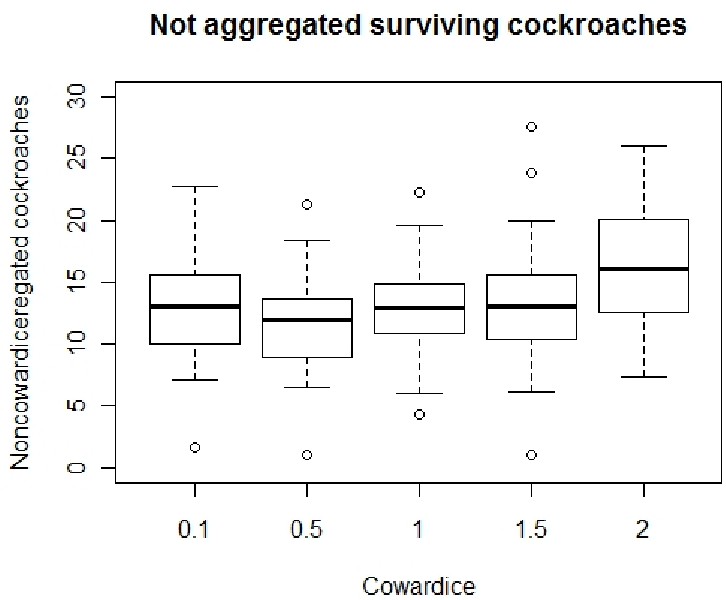

Figure 5.21: The percentage of not aggregated cockroaches in the last tick of Experiment 5.3.1. “Not aggregated cockroach” is a cockroach with less than three cockroaches closer than 2 space units.

5.5 Discussion

In this chapter, we have studied the impacts of cockroach aggressivity on their populations: their size, aggregation rate, etc. Our models suggest that reasonably high aggressivity leads to more cockroaches living in an environment and that it facilitates aggregation (see sections 5.4.2, 5.4.8, 5.4.10).

Discovering the explanation of this phenomenon is probably one of the most interesting results of this thesis. We have shown that when cockroaches are aggressive, more cockroaches die in aggregations[26], where they are easily found and consumed by other members of the aggregation. These other members do not have to leave the aggregation to find food elsewhere, which would lead to spending a lot of their energy on walking. Instead, they mostly sit (which is not as energetically expensive as walking) and when they become hungry, there is a chance there will be a corpse easily found in their vicinity. Then they simply eat the corpse and sit again. This way, when cockroaches need less energy in general to live, the spared energy may be, abstractly speaking, transformed into creating and sustaining further cockroaches in the cockroach habitat. The environment has limited resources, food being added to it limits the carrying capacity of the system. However, when agents use the limited energy more efficiently, more agents may be sustained.

It was important to know whether the cockroach aggressivity would not lead to cockroach asociality and nonaggregative behavior. After all, social cockroaches risk being eaten in an aggregation by other hungry aggressive cockroaches. That is precisely why we have made our models evolutionary, evolving cockroach sociality. With all tested values of aggressivity which did not lead to extinction of modelled cockroaches, cockroaches evolved as very social and aggregative (actually, reasonably aggressive cockroaches were even more aggregative than nonaggressive ones, see section 5.4.2, Figure 5.8), see 5.4.8. Therefore, we conclude that it is still advantageous for cockroaches to aggregate, even when they are aggressive.

Another question we asked ourselves when designing this model line was, why real cockroaches do not, when given a chance, slaughter one another. It seems that it simply is not worth it as shown by Model 5.3 and Model 5.3.1 where sociality and aggressivity were evolved together and the resulting aggressivity was by no means overly high, see 5.4.8 and 5.4.10. Too aggressive cockroaches burn too much[27] energy by attacking when it would be more effective for them to look around and move to a corpse of another cockroach for example.

Let us note that what exactly is “reasonably aggressive” depends on how we define the aggressivity in a model. In our model, a hungry cockroach looks on his the patch he is standing on, if there is food, he eats, if not, he tests whether he will not attack another cockroach. If he does not attack, he looks for food in his 4-neighbourhood. Another way of modelling the aggressivity would be that a hungry cockroach would first look on his current patch, if no food was there, in 4-neighbourhood and when no food would be there neither, he would test whether to attack another cockroach or not. “Reasonable aggressivity” was about 0.1-0.15 in

[26]Since cockroaches kill one another, there is obviously more deaths. Since aggressive cockroaches are aggregative, they often kill one another in an aggregation or nearby; this leads to more corpses in aggregations.

[27]Note that what is “too much” may depend on the energy price of cockroach attacks. If the price of attacking was lower, the aggressivity could be higher and still advantageous.

Model 5.0 or 5.3. If we had adopted the other approach (with a cockroach testing his aggressivity after looking in his 4-neighbourhood), the resulting aggressivity would be higher as a number, but the effect of cockroach aggressivity on the cockroach population would be, more or less, the same[28].

Further important result is that social aggressive cockroaches are capable of defending themselves well against invasions of other, different cockroaches (e.g., asocial, nonaggressive, highly aggressive etc.). It leads us to believe that they will probably defend better against other non-cockroach insects too.

The last interesting result we have obtained from model line 5 concerns seasonal food. We have shown that if there is an environment, where food grows seasonally (i.e., seasons of food being added to the environment are rotated with seasons of no food being added to the environment) and the season of starvation is long, then aggressivity leads to much higher survival rate of cockroaches. We may consider an aggregation of aggressive cockroaches to be something of a "fridge"[29]. When there is a season of no food grown, nonaggressive cockroaches spread in the environment searching for food. This way, they burn a lot of energy and their corpses are more difficult to find. On the other hand, aggressive cockroaches have their "fridge" – they sit a lot in their aggregations, when they become hungry, they kill someone (this is "taking a cockroach from their fridge"). Since it is almost useless to wander outside the aggregation anyway (only corpses of other dead cockroaches may be found after all the food from food season has been eaten), it is a great advantage that aggressive cockroaches are sitting in the aggregation and burn only a small amount of energy.

[28]Actually, we did such an experiment to show that our results are not totally dependent on our chosen model of aggressivity. Indeed, the results were qualitatively almost identical to results written in this thesis.

[29]The idea that this could happen has been suggested to us by Joanna J. Bryson.

6. Concluding remarks

In our thesis, we have tried to better understand the evolutionary reasons of cockroach aggregation. We have not concentrated on the well know explanation related to sexuality, but we have tried to find new possible reasons to aggregate instead. We have asked ourselves many questions concerning these reasons and tried to answer them.

We have used the NetLogo tool for our research as it is obviously not possible to study the cockroach evolution in real cockroaches and analytical models are not complex enough. The work we have done was very interesting. The subject of our research was purely of natural sciences but tools we have used came from computer science. Of course, we have discussed the design of our models with natural scientists. When creating models, it is often not the best way to make them as much biologically plausible as humanly possible. Such models are overly complicated and probably impossible to analyze. Instead, we tried to create models which are not implausible in important areas and which may be efficiently analyzed. Another positive aspect of using reasonably abstract models is that their results may be generalized and used for different entities also. It must be admitted though, that our results are results of computational models; they may represent reality but they may not represent it too. It is always a risk when using such models, it is best when they may be validated empirically. Nevertheless, if nothing else, these models provide an inspiration to natural scientists, where explanations of various phenomena may lie.

Let us (very briefly, see relevant chapters for more in-depth analysis) summarize our results:

One possible reason of cockroach aggregation formation, suggested by Model 1 is that it helps them to survive in an environment inhabited by predators. This result was expected, but our explanation is, to our knowledge, a new one. Usually, it has been thought that an aggregation is more difficult to find and that is the advantage of it. In our model however, aggregations are rather easy to find (when predators follow the chemical gradient generated by cockroaches in aggregations), but still advantageous as cockroaches create competition between predators. Predators then start killing one another when trying to get to cockroach aggregations.

Another possible reason lies in the area of necrocannibalism. We have shown that dead bodies of cockroaches are more concentrated in aggregations[1]. Cockroaches living in aggregations then have access to more food from dead bodies. In our models, dead cockroaches transformed into ordinary food. This alone made cockroaches aggregate. In nature however, necrocannibalism could be even more important as dead cockroaches are not only a source of food, but they are a source of food rich in proteins [8, p. 72]. Therefore, aggregating cockroaches would have more proteins in their food, which would confer a large advantage upon them (as opposed to asocial cockroaches eating various dirt).

In the last part of our research, we have studied cockroach cannibalism (willful attacking of other cockroaches with the purpose of eating them). It started as a small part of our research, but because the results were so interesting, it has

[1]It is mentioned in section 4.5.2, it is the fourth hypothesis in Additional research.

grown and it became the longest chapter of this thesis. At the beginning, we asked ourselves, how come that cockroaches survive when they kill one another? Why do they attack one another at all? We have shown that when cockroaches are not too aggressive, aggressivity leads to a slightly larger and better-eaten cockroach population than if they were nonaggressive. Furthermore, when we have let our modelled cockroaches evolve their sociality and aggressivity, they evolved into highly social and reasonably aggressive – which is how they are in nature[2]. The evolved population of highly social and reasonably aggressive cockroaches was slightly larger and noticeably better-eaten than modelled populations of social, yet nonaggressive cockroaches.

We consider this thesis important as we found a new (to our knowledge) explanation of cockroach aggregation formation: the necrocannibalism. Furthermore, we have studied cockroach aggressivity and succeeded in explaining why it is advantageous to cockroaches. Thus, we believe we have furthered the understanding of cockroach behavior. We have purposefully created our models generalizable. Our agents are named "cockroaches", but they may represent other insects too.

This thesis is also a testament to the capabilities of computer science helping natural sciences; it is likely that our results would be very hard to obtain by methods of natural sciences only.

6.1 Limitations of our research

Further work could be done on mechanisms of food addition in our models. During the two years we spend researching cockroaches, we have tried several other models of food growth (e.g., food generated according to Poisson distribution, more food growing in some places with no food growing elsewhere, etc.). When we have incorporated these mechanisms into our models, the difference from the currently used mechanism was only visual, if any. Statistical data we have collected were qualitatively unchanged. This does not mean though, that there is no mechanism of food growth which would not change the behavior of our models. It could be interesting to create a comprehensive set of various models of food growth in nature, test our models using them instead of the mechanisms currently used and watch how the behavior of modelled cockroaches changes.

Mainly Chapter 5 suffers from lack of additional statistical analysis. It is important to know whether the trends suggested by our graphs are statistically significant or not.

An inherent limitation of the method of multi-agent modelling is that it does not have to reflect reality. We have cooperated with natural scientists and tried to design our models in such a way that they do reflect reality, but unless we understand cockroaches perfectly, it is not certain that we have succeeded (and if we understood cockroaches perfectly, we would not need our models).

[2]Not all cockroaches varieties behave in such a way. However, we did concentrate on modelling varieties which do.

6.2 Future work and inspiration

The first two limitations (especially the second one) may be resolved. Resolving the limitation concerning the lack of additional statistical analysis is especially important.

Cockroach sexuality is another thing which could be studied further. We have largely simplified cockroach sexuality on purpose, if we have not done so, it would very likely make the analysis of our models difficult. It would be hard to tell whether cockroaches behave like they do because of sexuality or aggressivity or food-collection strategy, etc. However, now, when we know how our models work, if more plausible sexuality was added, we could study the effect of cockroach sexuality on their behavior in isolation.

Also, there are various state variables in our models. In case of some, we know how is the system sensitive to their change (e.g., we have observed how parameters change the behavior of the environment). However, in case of many constants, we could not try too many of their values. It would be interesting to know how changes of these affect the environment.

We believe that our models could be an inspiration to natural scientists too: The first model (with cockroaches and mantises) is not evolutionary and could be probably replicated with living cockroaches and mantises. An experiment suggesting the importance of cockroach coprophagy [15] has been made before. We believe that similar experiment could be done with cockroach corpses to show the importance of cockroach necrocannibalism. Also, the dependence of cockroach aggressivity on the amount of available food (and proteins in it) could be studied in nature.

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Appendix A: Input and output of models

This appendix contains an overview of input (parameters) of various models and their output (what is measured). This way, experiments described in the thesis may be replicated when the user sets the given parameters to values written in the thesis.

Furthermore, all experiments we have ran are currently saved in BehaviorSpace of each model. BehaviorSpace is a tool included in NetLogo for batch running of experiments and exporting their results. I.e., if the user of the given model wants to replicate our experiments, it is enough to re-run the experiment stored in BehaviorSpace memory. The following overview is included for people who want to run different experiments with our models. Both input and output may be modified.

The input consists of parameters of the model (we do not describe parameters already described in the thesis). Therefore, an user of the model may fix certain of these parameters (turning them into constants) or he may turn constants into parameters and see how different values of such a parameter (which was held fixed in our experiments) affects the results.

The output is measured using NetLogo internal procedures. To prevent misunderstanding, we include a short description of output values.

.1 Model 1

Input:

- `cockroach olfaction`
- `mantis repulsive range`

Output:

- `count mantises`: How many mantises were present in the environment in the last tick of the experiment.
- `count cockroaches`: How many cockroaches were present in the environment in the last tick of the experiment.
- `count mantises with hunger counter > 0`: How many nonhungry mantises were present in the environment in the last tick of the experiment.

.2 Model line 2

As the input of models 2.0, 2.1 and 2.2 is the same, as well as the output, we will write it once only.
Input:

- `food growth`

Output:

- `count cockroaches with sociality = 0, 1, 2, ..., 10`: This gives us the distribution of sociality among cockroaches.

.3 Model line 5

.3.1 Model 5.0

Input:

- `social aggressivity`

Output:

- `count cockroaches`: How many cockroaches were present in the environment in the last tick of the experiment.
- `mean sociality of cockroaches`: The average sociality of cockroaches
- `sum energy of cockroaches`: What is the total amount of `energy` in all surviving cockroaches at the end of the experiment.
- `100 * (count cockroaches with at least three other cockroaches closer than 2) / count cockroaches`:
- `walk moves`: How many cockroaches walked in the last tick.
- `sit moves`: How many cockroaches sat in the last tick.
- `eat moves`: How many cockroaches ate in the last tick.
- `attack moves`: How many cockroaches attacked in the last tick (note that a cockroach may both walk and attack in a single tick).

.3.2 Model 5.1

Input:

- `social aggressivity`
- `food age length`
- `starvation age length`
- `set-up`: This is not really a state variable, it is a technical variable instead, used to make the collection of results easier. The value of this parameter determines which subexperiment (see 5.4.3) is ran. If the value is 0, the user may set any allowed values of `food age length` and `starvation age length`.

Output:

- `count cockroaches`: How many cockroaches were present in the environment in the last tick of the experiment.

.3.3 Model 5.2

Input:

- `social aggressivity`
- `sociality`
- This is a technical variable, rather than a state variable; it is used to make the collection of results easier. The value of this parameter determines which subexperiment (see 5.4.5) is ran. If the value is 0, the user may create social, as well as asocial cockroaches with any allowed value of `aggressivity`.

Output:

- `count cockroaches`: How many cockroaches were present in the environment in the last tick of the experiment.
- `mean sociality of cockroaches`
- `mean aggressivity of cockroaches`: With the average cockroach aggressivity and sociality, we are able to determine which of two competing populations has won, which is precisely what we are interested in.

.3.4 Model 5.3

This model has no input as `aggressivity` of cockroaches is evolved.

The output of this model is the same as the output of Model 5.0.

.3.5 Model 5.3.1

Input:

- `cowardice`

The output of this model is the same as the output of Model 5.0.

Appendix B: Additional data for Model 1

.4 Number of aggregations formed

Table 1 describes how many aggregations are typically formed by 600 cockroaches in Model 1, depending on the value of `cockroach olfaction`. During measurement of these values, no mantises were present in the environment. The purpose of this table is to give the reader a general idea, how many aggregations is formed with a certain value of `cockroach olfaction`. The data of the table were collected by visual observation.

`cockroach olfaction`	aggregations formed
0	600
2	14-19
4	11-13
6	6-8
8	5
10	4
12	2-3
14	2-3
16	2
18	1-2
20	1

Table 1: How many aggregations were formed, depending on the value of `cockroach olfaction`.

.5 Variations of measured data.

As we used 3D graphs for depiction of our results, there was no way of representing the variation of our results. Therefore we present variations of all three observed variables in the following table exported from R software:

```
cockroach  mantis     count          count        count
olfaction  repulsive  cockroaches    mantises     nonhungry
           range                                  mantises

        0          0   284.9995960  4.73898990    5.0864646
        2          0   478.6060606  2.54707071    2.8819192
        4          0   539.1590909  2.61454545    3.3675758
        6          0   557.7369697  2.98222222    3.1111111
        8          0   603.2165657  2.57323232    2.2985859
       10          0   485.4039394  1.60191919    2.0266667
```

12	0	680.4180808	1.96969697	2.9074747
14	0	664.9955556	2.57323232	2.7511111
16	0	409.0521212	1.67383838	1.8257576
18	0	510.6509091	1.89282828	1.9167677
20	0	406.9591919	1.68323232	1.7014141
0	2	76.0521212	3.59707071	4.7777778
2	2	377.8165657	4.62989899	5.6933333
4	2	485.1849495	3.44757576	4.3086869
6	2	729.6565657	4.05090909	4.5555556
8	2	979.5470707	3.36363636	3.4488889
10	2	699.8711111	2.74131313	2.9696970
12	2	649.1995960	3.07262626	3.1049495
14	2	667.2786869	2.31626263	2.5490909
16	2	739.2059596	2.16676768	2.3308081
18	2	692.2339394	2.11272727	2.1796970
20	2	442.8581818	1.98828283	2.5514141
0	4	15.3958586	1.39181818	3.3660606
2	4	108.2718182	3.66656566	5.4621212
4	4	254.2031313	3.69808081	5.4650505
6	4	428.1102020	3.94909091	4.8226263
8	4	840.5142424	5.38131313	6.5102020
10	4	1083.6161616	5.78373737	4.9026263
12	4	1131.6440404	4.03747475	5.5930303
14	4	1008.6561616	5.08323232	5.8145455
16	4	1261.4435354	4.47222222	4.8172727
18	4	955.5620202	4.13696970	3.7449495
20	4	690.0075758	2.27020202	2.4293939
0	6	5.6096970	0.12161616	4.0132323
2	6	40.6112121	1.62626263	5.7069697
4	6	80.7146465	2.26101010	7.3190909
6	6	300.7049495	4.25242424	6.1110101
8	6	577.9970707	5.15595960	7.0192929
10	6	1001.1903030	6.09080808	8.1877778
12	6	1320.4925253	8.19191919	8.8888889
14	6	1744.6435354	6.52686869	6.9368687
16	6	1329.7271717	6.46252525	6.0988889
18	6	1458.5147475	7.65090909	8.5021212
20	6	1000.1276768	3.51515152	3.5418182
0	8	3.3675758	0.09888889	0.4988889
2	8	31.2019192	1.28282828	5.5897980
4	8	63.3571717	2.08727273	6.1337374
6	8	297.4440404	3.31909091	7.1211111
8	8	642.1837374	5.37080808	8.9166667
10	8	775.8273737	4.98020202	8.0266667
12	8	1602.2904040	8.97818182	9.7635354
14	8	1479.2145455	7.07070707	7.3384848
16	8	1288.0707071	6.87030303	6.7001010
18	8	1670.4132323	9.11353535	7.9256566

20	8	1549.9526263	6.14656566	6.0221212
0	10	4.0075758	0.18777778	0.3838384
2	10	25.3877778	0.83585859	4.6642424
4	10	65.0273737	1.62060606	5.5631313
6	10	226.9069697	3.74494949	10.2596970
8	10	578.8964646	3.87434343	5.7061616
10	10	1114.9772727	6.39555556	8.3978788
12	10	1625.3352525	7.33444444	9.4112121
14	10	1657.2864646	7.58949495	9.5397980
16	10	1334.5506061	7.53535354	8.2561616
18	10	1873.9696970	8.11424242	7.7312121
20	10	1318.5151515	4.63272727	4.0339394
0	12	2.4892929	0.16272727	0.3364646
2	12	25.2172727	1.93575758	6.1893939
4	12	75.4677778	2.20313131	4.6071717
6	12	218.8945455	3.01767677	6.1559596
8	12	507.6985859	4.11020202	8.1818182
10	12	1249.6867677	5.75141414	8.1717172
12	12	2270.4988889	9.48040404	10.9586869
14	12	1798.9107071	7.48797980	8.1195960
16	12	1201.3796970	6.87919192	7.2367677
18	12	1929.5631313	9.44888889	9.8787879
20	12	1502.6690909	4.14656566	4.5061616
0	14	0.8387879	0.13575758	0.2440404
2	14	36.4786869	1.37212121	4.3574747
4	14	73.9802020	1.64404040	4.9061616
6	14	239.4322222	3.13727273	6.3445455
8	14	674.1893939	4.53121212	8.1660606
10	14	940.1919192	6.06818182	9.2576768
12	14	1677.6172727	7.18494949	8.9110101
14	14	1366.2206061	7.14141414	8.8342424
16	14	1698.9344444	8.40595960	10.3566667
18	14	1843.6266667	8.27717172	9.9393939
20	14	1115.1511111	4.47232323	3.6819192
0	16	0.6953535	0.15595960	0.4342424
2	16	29.4056566	1.31959596	6.4400000
4	16	83.0682828	2.27020202	4.5586869
6	16	254.4892929	3.09282828	7.2925253
8	16	583.8928283	4.64404040	7.5485859
10	16	852.5349495	4.92363636	9.5555556
12	16	1593.6746465	6.60767677	9.1187879
14	16	1974.8253535	7.12434343	9.2020202
16	16	1078.6610101	7.45454545	8.2403030
18	16	1700.2095960	8.06575758	8.8358586
20	16	1176.2448485	3.27636364	3.9410101
0	18	1.9288889	0.13575758	0.3208081
2	18	31.0913131	1.35949495	5.2196970
4	18	76.8117172	2.13444444	4.2622222

6	18	215.5615152	2.39393939	4.7049495
8	18	610.2273737	5.06050505	7.0726263
10	18	1148.8665657	6.18343434	9.4016162
12	18	1567.1195960	6.88272727	8.8156566
14	18	1599.7802020	7.07070707	7.6827273
16	18	1991.3635354	7.97282828	8.5252525
18	18	1789.8787879	6.99636364	6.9923232
20	18	1343.4314141	5.49333333	3.7511111
0	20	1.2019192	0.18292929	0.4261616
2	20	44.6596970	1.66979798	6.3721212
4	20	70.5842424	1.56202020	5.0985859
6	20	212.7559596	2.93686869	7.7998990
8	20	542.3243434	3.80646465	7.2985859
10	20	767.5857576	5.48323232	10.3453535
12	20	1254.2475758	6.47434343	8.6460606
14	20	1352.0859596	5.91272727	7.9065657
16	20	1611.5970707	8.84848485	10.6031313
18	20	1803.8319192	10.33080808	9.8480808
20	20	1417.7837374	4.45848485	3.9469697